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THE SHELL STRUCTURE OF CHONETACEAN BRACHIOPODS AND THEIR ANCESTORS

1 SEP 1972

C. H. C. BRUNTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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THE SHELL STRUCTURE OF CHONETACEAN BRACHIOPODS AND THEIR ANCESTORS

BY

HOWARD BRUNTON

Pp. 1-26; 9 *Plates,* 8 *Text-figures*

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In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

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ADDENDA ET CORRIGENDA

p. 6, caption to Fig. 2
The inhalant current arrow should have a flight on its tail, the exhalant current arrow no flight.

p. 7, paragraph 3, line 1
For "teleolae" read "taleolae".

p. 9, caption to Fig. 3B, line 3
An arrow without a flight should be inserted before "exhalant current".

p. 24
For "Grant, R. E. (in press)" read "Grant, R. E. 1972. The lophophore and feeding mechanism of the Productina (Brachiopoda). *J. Paleont.*, Tulsa, **46** : 213–48, pls 1–9".

p. 25
The reference after Williams, A. 1968, should be Williams, A. 1969. The book was published by the University of Wales Press not "aloes". The reference following should be Williams, A. 1970.

p. 25
Under "Locality details of figured specimens", the second name should read "*Leptelloidea leptelloides*" not "*Leptelloides leptelloides*".

THE SHELL STRUCTURE OF CHONETACEAN BRACHIOPODS AND THEIR ANCESTORS

By C. H. C. BRUNTON

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SYNOPSIS

The criterion of shell microstructure has been added to general morphological considerations in this study of possible ancestors for the Chonetacea. The results support Havlíček's suggestion that the sub-family Aegiromeninae was the plectambonitacean stock from which the first chonetacean evolved in the late Ordovician. Ordovician to Permian chonetaceans have been studied and the observed changes in their shell structure are discussed. Functional morphological interpretations are presented and consideration is given to the significance of spines in these brachiopods.

I. INTRODUCTION

During the past ten years or so there have been several notable publications on the Chonetacea. The origin and phylogeny of the group has always been problematical, for, as Muir-Wood wrote in 1962, 'More research requires to be done . . . if the relationship of these very numerous and wide-spread forms is to be established.' She briefly discussed chonetacean origin indicating that she favoured the Plectambonitacea as ancestors, but reminded readers of Paeckelmann's suggestion (1930) that the chonetids were derived from a strophomenid stock.

More recently Boucot & Harper (1968) have revised Silurian and Lower Devonian Chonetacea, but restricted themselves to phylogeny within the group and made no comment upon ancestry. However, Havlíček (1967) while discussing the evolution of the Sowerbyellidae '. . . assumes *Chonetoidea* to be incontestibly the direct precursor of the superfamily Chonetacea . . .'. Havlíček derives *Chonetoidea* from an *Aegiromena* stock whilst *Eochonetes* is derived from the *Sowerbyella* stock. In his view, therefore, *Eochonetes* is not in the group ancestral to the chonetaceans as I had implied in 1968.

Thanks to the stimulus provided by the work of Williams, especially his shell structure study of 1968 which formulated a framework for future research, we are now in a better position to apply detailed examinations of shell microstructure to the problems of phylogeny in a meaningful fashion. Williams interpreted the shell microstructure of the Chonetidina, Productidina and Strophomenacea as being fundamentally the same, (i.e. entirely laminar) while that of the Plectambonitacea differs in retaining a fibrous secondary layer. In his phylogenetic chart Williams (1968) derived the chonetids, productids and oldhaminids from the Strophomenacea, which in turn, along with the Davidsoniacea and 'probably the triplesiidines' he derived from the Plectambonitacea by a process of neoteny: the laminar shell of the strophomenides being homologized with the laminar primary layer of the plectambonitaceans.

We are left, therefore, with the need to investigate the possibilities of chonetids being derived either from plectambonitaceans involving a change of shell structure, or from the strophomenaceans, with which they appear to have a common shell structure.

Clearly, in any such study the more factors investigated the better. I believe the microstructure of the brachiopod shell to be so intimately bound up with the metabolism of the living organism as to be of profound importance systematically; nevertheless, it is vitally important to consider closely the gross morphology of the valves so as not to suggest evolutionary relationships involving highly improbable morphological changes. The purpose of this study is the detailed investigation of the chonetacean shell microstructure, together with that of their possible ancestors, in the hope of resolving the early phylogeny of this group, the evolution of which took place during Upper Ordovician times.

I retain here the view expressed in 1968 that the Chonetacea should be classified more closely to Productacea than, for instance, to the Strophomenacea. The removal of the Cadomellacea from Muir-Wood's suborder Chonetidina (Cowen & Rudwick 1966) leaves only the Chonetacea, and, at present, I am in favour of leaving the situation fluid to the extent of retaining the Chonetacea as a superfamily within the Strophomenida and not using the term Chonetidina. The Productidina usefully unites several superfamilies which have reasonably established morphological characteristics in common. The Strophomenida as a whole is an order within which there is room for phylogenetic reappraisals, e.g. the removal of *Thecospira* and *Cadomella* (Brunton & MacKinnon, in press), and introduction of the Triplesiacea and Thecideacea, problems upon which several palaeontologists are engaged and have already commented (Cowen & Rudwick 1966, Williams 1968, Rudwick 1968, Wright 1970, Mr. D. McKinnon personal communication January 1971).

II. MORPHOLOGY

The most recent and complete description of chonetaceans is that of Muir-Wood (1962). Several aspects of their morphology have been discussed (Brunton 1968) but further work now necessitates some revision.

The main point of departure from the views expressed in 1968 concerns the possible reconstruction of the lophophore (1968, text-fig. 50). At that time the traditional idea of a spirolophe for chonetaceans was followed. However, more recent studies on this group, productaceans, strophalosiaceans and thecideaceans leads to the opinion that the lophophore in these fossil groups consisted of a schizolophe or variously lobed forms of a ptycholophe. In the sense of Williams & Rowell (*in* Williams *et al* 1965 : H37–8) it is a lobed trocholophe because the lophophore is believed to have had only a single series of filaments, as in Recent *Thecidellina*, rather than the more complex double filaments characteristic of most other Recent lophophores from the schizolophous to plectolophous stages. Rudwick (1968) reminds us that the terminology employed to describe lophophores was based originally upon the arrangement of the brachial axis without consideration for the number of filament rows. Thus whilst phylogenetically there is logic in Williams and Rowell's terminology (1965, H38), it is less confusing to retain the previously existing definitions qualified, where necessary, to indicate if the filament series is double or single. Believing that the thecideaceans may be remnants of the Strophomenida, derived from a productidinid stock not far removed from *Cooperina* Termier, Termier & Pajaud 1967 (but see Cooper & Grant 1969), it is logical to interpret the chonetacean lophophore as having been only a single row of filaments (Text-fig. 1). In his study of the Triassic brachiopods *Thecospira* and *Bactrynium*

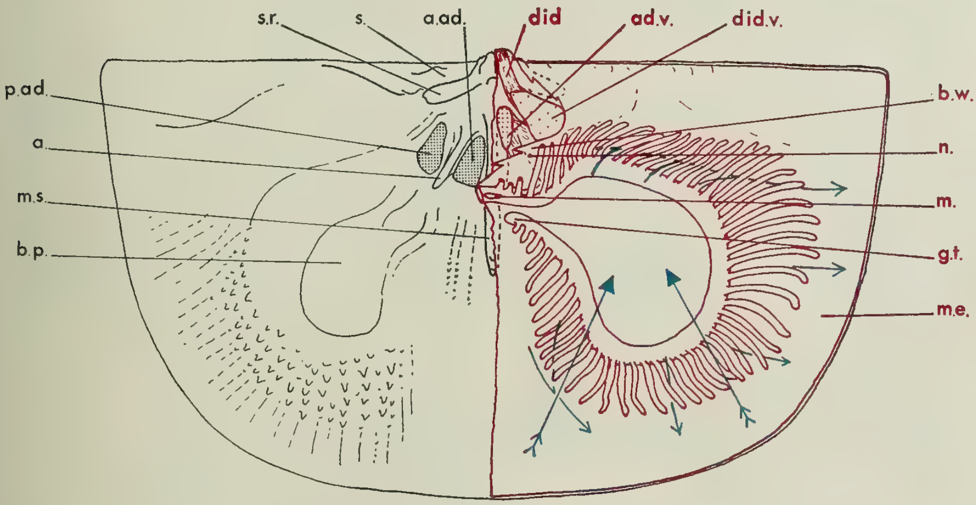

FIG. 1. Diagrammatic dorsal valve interior of a chonetacean showing, on the left, general morphology and, on the right, the inferred anatomy and suggested water currents associated with the lophophore, a. – anderidium; a.ad. – anterior adductor muscle scar; ad.v. – adductor muscle, ventral attachment area; b.p. – brachial platform; b.w. – inner epithelium of the body wall separating the brachial cavity from the visceral cavity. The epithelium of the visceral cavity has been cut ventro-medianly to expose the muscles; did. – diductor muscle; did.v. – ventral attachment area of the diductor muscle; m. – mouth; m.e. – mantle epithelium; m.s. – median septum; n. – possible position of the nephrostome in the body wall, excreting into the posterior exhalant current; p.ad. – posterior adductor muscle scar; s. – socket; s.r. – socket ridge; ↠ inhalant and → exhalant feeding/respiratory water currents.

Rudwick (1968) discussed their affinities with the Thecideacea and the general phylogeny of that superfamily. He accepted the Termiers' & Pajaud's (1967) assignment of the Permian genus *Cooperina* to the Thecideacea, so that it became the earliest representative of the superfamily, which he considered as derived from a Lower Permian or even earlier davidsoniacean. Study of *Cooperina* shows that Cooper & Grant (1969) are correct in placing the genus in the Strophalosiacea and it seems that the morphological evidence presented by Rudwick for a derivation from the Davidsoniacea is better met by the Strophalosiacea, a group believed to have diversified widely and to have given rise to both the Richthofeniacea and Lyttoniacea. Rudwick (1968, 1970) related the Lyttoniacea and Thecideacea to the Davidsoniacea.

While preparing this paper I was privileged to be shown the script of a paper by Grant (in press) in which he describes a calcified 'ptycholophous brachiophore' in Permian Productidina (ptycholophous here used as by Grant in the morphological sense of being several lobed). The interpretation of this structure supports the contention that the brachial ridges of Productidina do indeed mark the positions to which the lophophore was attached in the living animal and that the 'ptycholophous' (or multilobed trocholophous) lophophore described by Grant evolved as a specialization from the more generalized schizolophe or simple ptycholophe characteristic of many Strophomenida.

A study of particularly well preserved Pennsylvanian and Permian chonetacean interiors in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, shows that in some rugosochonetids and species of *Dyoros* the antero-median tuberculation of the brachial ridges merges into the anterior end of the median septum. In some thickened (? old) specimens of *Dyoros* the anterior end of the median septum is winged laterally in such a way as almost to bridge the gap between it and the brachial ridges (Text-fig. 2). The exaggerated development of tubercules and prolonged deposition of secondary shell in the regions of the brachial

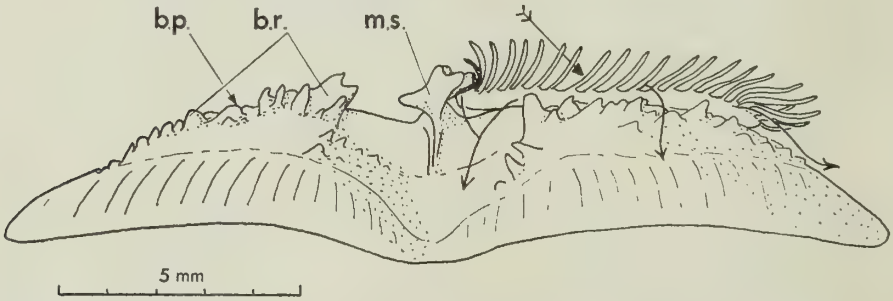

FIG. 2. Anterior view of *Dyoros* sp. (Chonetacea) dorsal valve from the Permian of Texas illustrating the highly tuberculate brachial ridges and anteriorly winged median septum. The inferred position of the lophophore and feeding water currents are added on the right. → inhalant current; »→ exhalant current; b.p. – brachial platform; b.r. brachial ridge, m.s. – median septum.

ridges and median septum probably resulted from the stresses imposed by the lophophore upon the secretory mantle epithelium in these areas. It may have been simply the weight of the lophophore hanging from the dorsal valve that induced this additional shell secretion in those specimens living in a position with their dorsal valves uppermost.

The chonetacean lophophore is envisaged as having been suspended from the dorsal inner epithelium with the postero-median mouth segment attached to the body wall between and probably ventral to its support by the anterior tips of the anderidia (= lateral septa of Muir-Wood 1962). The strong tuberculation of the brachial ridges probably reflects the strong attachment of the mantle to the shell where it supports the lophophore (Text-fig. 3). Antero-medianly the generative tips of the lophophore probably recurved posteriorly onto the median septum (Text-fig. 1); however, it is impossible to say whether they remained separated by the septum or united in the median plane as in living *Megathiris*.

The relationship between pseudopunctae and teleolae requires clarification. In the brachiopod volume of the Treatise (1965 : H420) Muir-Wood incorrectly redefined the term taleolae, specifically as applied to chonetids, saying that they had a 'central cavity'. In observing many taleolae under the scanning electron microscope a central cavity has never been observed. It may be that the impression of such a structure resulted from optical effects or that the cavities were those of rib apertures.

Taleolae, as defined by Williams (1956), are rods of calcite in the axial position of many pseudopunctae (Pl. 1 figs 1, 2). Taleolae are found neither in all pseudopunctae nor necessarily forming the core to the complete pseudopunctum in which they occur. When absent the shell layers or fibres can be traced into the centre of the structure, which is composed of inwardly and commonly anteriorly directed conical flexures producing tubercules on the inner surfaces of the valves (Pl. 1, fig. 4). This structure contrasts with the outward flexures of shell fabric surrounding endopunctae (Brunton 1969, fig. 11, 1971; pl. 11, figs 8, 10). The pseudopunctae of upper Palaeozoic chonetaceans have taleolae while those of geologically older specimens are without, or with only weakly developed taleolae. Baker (1970) describes *Moorellina* specimens within which the pseudopunctae differ in character; those of the dorsal valve have cores of primary shell resembling taleolae, whilst those of the ventral valve are without and composed entirely of radially disposed bundles of secondary fibres.

In 1968 the author's text-figure 45 indicated that he interpreted the sub-median ridges in the ventral valves of some chonetids as being the traces of mantle canals. It is now believed that in some narrow-bodied species with thickened shell these ridges developed in the regions bordering the ventral edge of the dorsal median septum. In such specimens the brachial cavity of the closed shell would have been divided almost completely into two chambers. The significance of this is not clear and the relationship of these ridges to mantle canal traces is in doubt; the effect, however, is similar to that of mantle canals, viz. the pressure of a structure onto the internal epithelial surface inhibiting shell deposition with increased shell thickening on either side.

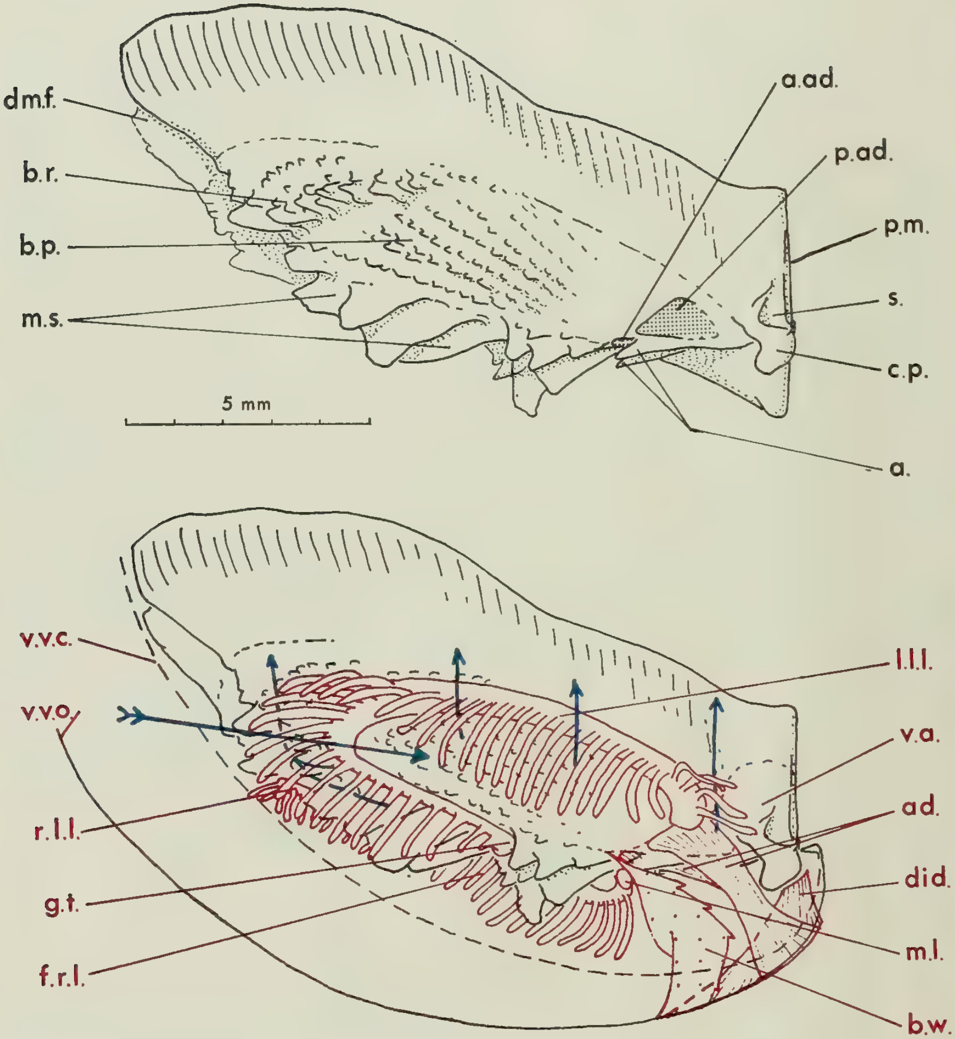
dm.f.
b.r.
b.p.
m.s.
a.ad.
p.ad.
p.m.
s.
c.p.
a.
5 mm
v.v.c.
v.v.o.
r.l.l.
g.t.
f.r.l.
l.l.l.
v.a.
ad.
did.
m.l.
b.w.

FIG. 3A. Ventro-lateral perspective view of the dorsal valve interior of *Dyoros* sp. from the Permian of Texas illustrating the surface morphology.
a. – anderidia; a.ad. – anterior adductor scar; b.p. – brachial platform; b.r. – brachial ridge; c.p. – cardinal process; dm.f. – dorso-median fold; m.s. – median septum (here strongly tuberculate); p.ad. – posterior adductor scar; p.m. – posterior margin of valve; s. – socket.

If one ignores the Daviesiellidae, in particular *Daviesiella* and *Airtonia*, and *Chonostrophia* (which may not be a chonetacean) the Chonetacea are morphologically conservative from their origins in the Upper Ordovician to the topmost Permian. Normally they share a gently concavo-convex profile, multicostellate ribbing, low interareas set at a wide angle from each other and several pairs of more or less posteriorly directed hollow spines on the posterior margin of the ventral valve. Teeth, sockets and socket ridges are developed, and in the dorsal valve the adductor scars commonly are divided by a ridge (anderidia). The cardinal process is low, internally bilobed in early forms but tending to become knob-like and commonly trifid externally; the median septum is only high anteriorly and developed late in ontogeny. The pseudopunctate shell manifests itself internally by tubercules. At least in early stages of ontogeny several genera were attached to the substrate by a thin apical pedicle protected by a shelly sheath.

III. ANCESTRAL STOCKS

At first sight certain strophomenaceans seem suitable as ancestors to the Chonetacea; general shape and size of some stropheodontids seem correct, as are features such as the dorsal valve protegulal node and development of a pedicle sheath on such genera as *Pholidostrophia*. Williams' 1968 investigations indicated that the shell structure is comparable in both groups, i.e., essentially laminar. However, it is shown below that the shell structures differ and the above characteristics are common to the Strophomenida.

Previous morphological studies have shown that many features are shared by the Plectambonitacea and Chonetacea with the result that several palaeontologists (e.g. Chao 1928, Sarycheva & Sokolskaya 1959, Muir-Wood 1962, Havlíček 1967) have thought these superfamilies to be phylogenetically related.

Strophomenacea, Plectambonitacea and Chonetacea obviously share strophomenid characteristics, but whilst doing so certain features of the Chonetacea tend to be more akin to those of the Plectambonitacea, especially the Sowerbyellidae, than to the Strophomenacea. Thus the Sowerbyellidae and Chonetacea share similar shell profiles and outlines and do not include the same elaboration of shell shapes met

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FIG. 3B. Inferred principal anatomy added to the above specimen (in red) and possible ciliary induced water-current through the lophophore (in blue). ⇛→ Inhalant current; exhalant current; ad. – adductor muscle, divided dorsally by anderidium; b.w. – body wall with left side removed to expose visceral cavity; did. – diductor muscle; f.r.l. – filaments of right lophophore lobe; g.t. – generative tip of lophophore; l.l.l. – left lobe of lophophore; m.l. – mouth (median) segment of lophophore, cut on left to expose muscle bases; r.l.l. – right lobe of lophophore; v.a. – left visceral region; v.v.c. – position of the interior of the ventral valve when the shell was closed; v.v.o. – inferred relative position of the ventral valve when the shell was open by about 20°. N.B. This reconstruction is not intended to imply a ventral movement of the ventral valve when the shell opened. Other than a portion of the body wall, epithelial layers, such as the mantles, are not depicted and it should be remembered that epithelia would have covered all the internal shell surfaces illustrated.

within the Strophomenacea. Similarly with external ornamentation, save that accentuated costae common to several sowerbyellid genera are only hinted at in the oldest chonetacean genus, *Strophochonetes*.

Early and mid-Ordovician Plectambonitacea are more varied in shell shape and it seems that the Strophomenacea inherited this tendency to variety. By upper Ordovican times shell shape was more stable in Plectambonitacea and from such a stock the Chonetacea inherited their conservative outline and profile.

Within the dorsal valves of sowerbyellids are paired ridges lateral to the mid-line or median septum, which is low or absent posteriorly leaving a cavity at the base of the cardinal process; a cavity interpreted as that of the brephic valve. These features are more common to the chonetaceans than to strophomenaceans. In Plectambonitacea the ridges ('inner' and 'outer side septa' and 'bema' of Cocks 1970) may be homologized with the anderidia, accessory septa and brachial ridges of chonetaceans. The pit at the base of the cardinal process is the alveolus of chonetaceans.

Whilst some Strophomenacea share some of these features, as well as denticulate hinge lines, their general combination is more in keeping with Sowerbyellidae and Chonetacea. Furthermore, some mid- and upper Ordovician Sowerbyellidae, e.g. *Eochonetes*, *Chonetoidea*, possibly *Sentolunia*, have hollow canals in the ventral valve posterior margin which are closely comparable to the spine canals of chonetaceans. Havlíček (1967 : 38) suggested that these canals may have accommodated hold-fasts used to attach these plectambonitaceans to seaweed.

On looking at mid- to upper Ordovician faunas for possible chonetacean ancestors it seems that the morphological requirements may best be met by the Sowerbyellidae.

IV. PLECTAMBONITACEA

Since this study was started Cocks has published on Silurian Plectambonitacea (1970). His paper contains useful and interesting discussion on functional morphology, but not all his suggested reconstructions of the musculature and feeding mechanisms are accepted here. These operations have important implications upon the way in which the plectambonitacean/chonetacean shells are envisaged as having been organized. Whilst agreeing to the possibility of the shells being able to snap shut as a defence mechanism and possibly also as a repositioning mechanism, it is difficult to envisage a brachiopod habitually feeding by pumping water through its brachial cavity by means of a flapping valve system such as proposed by Rudwick (1961) for Richthofenacea and invoked by Cocks. A ciliary induced water current seems to be a well tried, stable and energy conserving system widely used in invertebrates and invariably used in extant brachiopods. By whatever means a water current is produced its function is to provide for respiration and feeding. Evidence suggests that a lophophore is required for these purposes, even allowing for the possibility of feeding on dissolved nutrients as proposed by McCammon (1969) and it seems likely that the plectambonitaceans, even the structurally specialized *Eoplectodonta*, retained a lophophore capable of a normal ciliary beat.

It may be unwise to compare a living genus so widely separated from the

Plectambonitacea taxonomically, but the dorsal internal morphology of *Megathiris* has, what are believed to be, analogous structures. In *Megathiris* the quadrilobed ptycholophe, with a single series of filaments, is supported by a calcareous loop partially fused to three ridge-like pillars which are prominent anteriorly. The loop, and thus the lophophore, is a few millimetres behind the anterior faces of these ridges (see Treatise 1965, H 836 for fig.). The lophophore does not project posteriorly along these ridges to the extent that might be supposed from Atkins' figure 6 (1960, – her figure 7 gives a clearer impression of the true situation) which is reproduced in the Treatise (Williams *et al* 1965, fig. 41). The body wall, behind which the muscles and viscera are situated, extends antero-dorsally between these ridges as a dissected plane at approximately 45° to the commissural plane and following the postero-dorsal side of the loop. In this way the anteriorly exaggerated median septum and pair of ridge-like pillars lift the lophophore from the dorsal valve floor allowing the antero-median extension of the body cavity, including dorsal adductor muscles. It is thought that the plectambonitacean morphology, exemplified by *Eoplectodonta*, achieved similar results.

The socket ridges, of Williams, or clavicular plates, of Cocks (1970) are considered to have functioned as postero-lateral supports to the body wall in the region of the mouth segment of the lophophore, much as were the opinions of Kozlowski (1929) and Öpik (1933), (As the principal points of pivot in these shells occurred at the posteromedian surfaces of these structures the term socket ridge is favoured). In this respect *Eoplectodonta* displays a feature common to many of the articulate-brachiopods, that of a close relationship between articulation and support of the body wall in the region of the lophophore.

The plectambonitacean lophophore probably followed the lateral edges of the bema (Cocks), or lophophore platform (Williams), so that a variously modified ptycholophe, in which the generative zone (or zones) recurved postero-medianly, was suspended from the dorsal mantle. Assuming a ciliary induced water current from the brachial lip across the filamentous area of the lophophore, a circulation may have been achieved in which water entered ventrally, perhaps particularly medianly, and passed out dorsally, close to the dorsal valve and especially laterally (Text-fig. 4). There seems little good reason why many of the later plectambonitaceans, those that had reduced their teeth, could not have had a wide gape while feeding. A wide gape might be advanced as the reason for very large, anteriorly extended, dorsal adductor muscle scars (Text-fig. 5), rather as is the situation in *Megathiris* today, which opens to about 45° or *Thecidellina* opening more than 60°. Whether or not the dorsal adductor scars of *Eoplectodonta* covered the bema, as suggested by Cocks (1970), it seems clear that these areas and those between the two pairs of septa on the dorsal valve, accommodated body tissues and that the lophophore was elevated on these septa. However, as in *Megathiris*, the lophophore probably did not follow the septal crests because in heavily thickened shells the septa may touch the interior of the ventral valve when the shell is closed, leaving little or no space for the brachial axis.

The morphology of the geologically older (Ordovician) plectambonitaceans is indicative of a schizolophe and perhaps only in geologically younger members of the Sowerbyellidae did the lophophore evolve into a quadrilobed structure.

In various Ordovician species of *Anoptambonites* and *Bimuria* there is muscle scar evidence for the dorsal adductors being restricted posteriorly, in a more traditional position, and these scars are divided by raised areas which may be homologized with Cocks' 'outer side septa' and possibly with the anderidia of chonetaceans.

It is believed that the Sowerbyellidae, particularly *Eoplectodonta* and *Plectodonta*, were specialized plectambonitaceans which nevertheless retained essentially normal systems of feeding. Their 'cousins', the Aegiromeninae remained more generalized and are morphologically more suitable to have provided the stock from which chonetaceans evolved.

The Aegiromeninae tend to be small-sized shells, commonly about 10 mm. wide, gently concavo-convex with shorter interareas and more regular ribbing than the Sowerbyellinae. Socket ridges are reduced and the dorsal median septum does not extend posteriorly to the cardinal process but appears to be flanked by the adductor

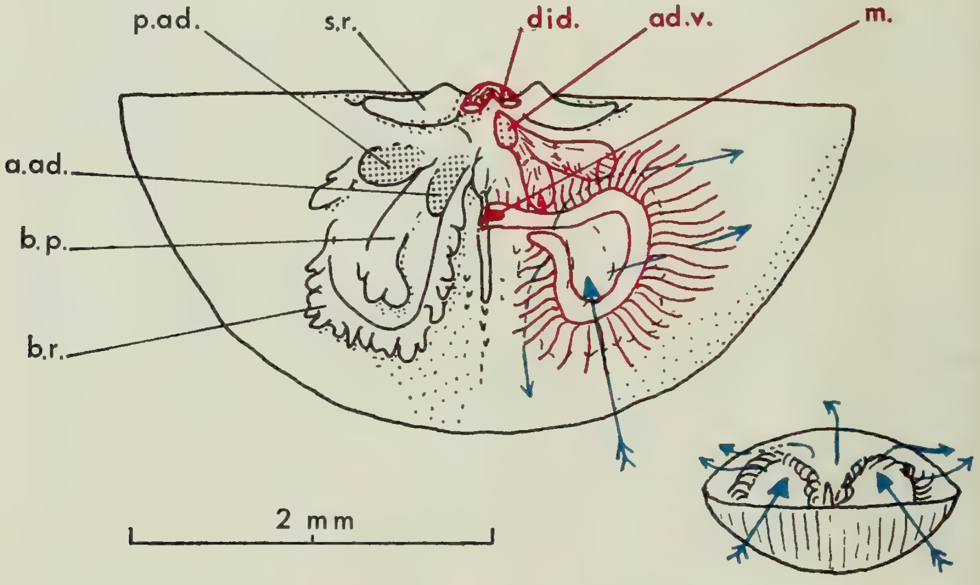

FIG. 4. Stylized illustration, based on *Bimuria siphonata* Cooper, from the mid-Ordovician of Pratt Ferry, Alabama, showing the internal dorsal valve morphology on the left with the inferred lophophore and main muscles on the right (red). The blue arrows indicate the main circulation of water through the lophophore, and this is further illustrated by the small diagram of an open shell, viewed posteriorly, on the right. (The dorsal valve is uppermost and water enters from the front) a.ad. – anterior adductor scar; ad.v. – ventral attachment area of adductor muscle; b.p. – brachial platform; b.r. – brachial ridge; did. – diductor muscle; m. – mouth; p.ad. – posterior adductor scar; s.r. – socket ridge.

muscle scars and variously placed elongate tubercules which may have assisted in the support of the lophophore. There is a complete lack of the strong dorsal internal ridging typical of the Sowerbyellinae and Leptellinidae and this morphology is entirely suitable as being ancestral to the sparsely featured early chonetacean dorsal interiors.

V. SHELL STRUCTURE

Plectambonitacea

Morphologically the Sowerbyellinae form a closely knit subfamily. The shell structure of the genera investigated (*Sowerbyella, Viruella, Eoplectodonta, Thaerodonta, Plectodonta* and *Eochonetes*) supports this unity. In these genera the secondary shell layer is standard in that the fibres show an internal mosaic (Pl. 1, fig. 4) and the typical cross-sectional stacking (Pl. 2, figs 1, 2) familiar within Recent terebratulids and rhynchonellids. The outer primary layer appears to be more variable, thin and commonly poorly preserved, and may be differentiated simply as a layer of much smaller 'fibres' (Pl. 2; figs 3, 6). These outer elements do not seem to show the brick-like cross-section or lateral fusion that would be expected in a lamellose fabric. Taleolae are not strongly developed in the pseudopunctae of these shells.

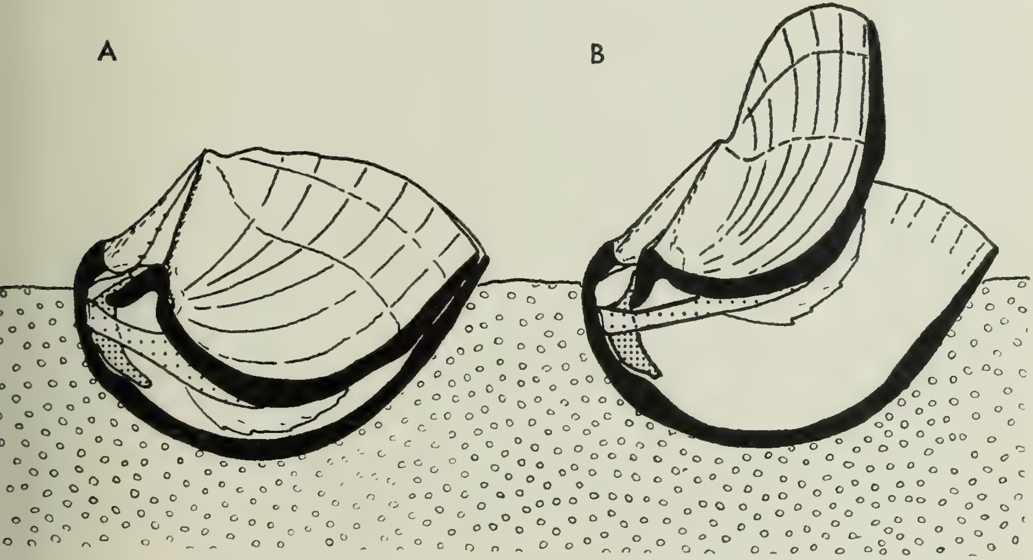

FIG. 5. Median longitudinal section of *Eoplectodonta* showing the inferred adductor and diductor muscles as they might have been when the shell was shut (5A) and open with a gape of 45° (5B). The ventral attachment area of the adductor muscle (coarse stippling) is close to the median plane whilst the dorsal attachment area is between the submedian septum (or inner side septum), here omitted, and the outer side septum, seen beyond the muscle.

An unexpected structure shows in the shell of particularly well preserved *Eoplectodonta transversalis* (Dalman) specimens from the uppermost Llandovery of Gotland. The pseudopunctate secondary layer also has small endopuncta-like canals of about 3 μm diameter surrounded by small outward deflections of the fibres producing a cone-in-cone structure (Pl. 3, figs 2, 3) contrasting with that of the pseudopunctae. It is not yet known to what extent these small endopuncta-like structures pervade the shell and it has only been possible to trace any one of them over a distance of about 80μm through the secondary layer. They run subparallel to the pseudopunctae and it seems, therefore, that they were controlled by anteriorly migrating points of outer epithelium as distinct from the fixed positions of caeca around which the epithelium moved.

The subfamily Aegiromeninae seems rather more varied in its shell structure, as judged by evidence from *Aegiromena*, *Aegiria* and *Sericoidea*. Within this subfamily the shell structure differs from other Sowerbyellidae.

In *Aegiromena aquila* (Barrande), from the middle Ordovician of Czechoslovakia, the secondary shell is not entirely composed of standard fibres. Whilst retaining a well-separated, independent appearance, as if having been encased within organic sheaths during life, the typical fibre cross-sectional shape has almost been lost; only in rare instances (Pl. 3, fig. 5) can such fibres be distinguished and these tend to be towards the outer surfaces of the valves i.e. they were formed at early stages in the growth of the shell. Normally the fibres are about 14μm wide and elliptical in cross-section, their edges overlapping adjacent fibres to various extents (Pl. 3, fig. 5). The shell fabric is strongly pseudopunctate and these normally have taleolae (Pl. 4, figs 1, 2). Towards the external surface of valves the fibres are of a slightly smaller dimensions and tend to be thinner. A strongly differentiated primary layer has not been recognized, if indeed it ever existed, but these smaller external fibres may indicate a gradation from a thin laminar primary layer to the fibrous secondary layer.

Aegiria grayi (Davidson) from the Wenlock Shales of Dudley, England, is sparsely pseudopunctate and the fibres of the secondary layer retain a rather more standard appearance (Pl. 4, fig. 3). In these respects the species is somewhat more akin to the Sowerbyellinae, but the general morphology would not warrant a change to this subfamily. Primary shell was not distinguished in the material studied.

In *Sericoidea restricta* (Hadding) from the Caradoc of Girvan, Scotland, the sparsely pseudopunctate secondary layer shows virtually no sign of retaining standard fibres. The 'fibre' units within the shell appear to be well separated, as if formed in the standard manner within organic sheaths, and are of comparable dimensions (25-30 μm wide and 3–4 μm thick). Orientation of the 'fibres' remains subparallel from layer to layer (Pl. 4, fig. 4, Pl. 5, fig. 1), thus retaining the organization of the standard regime rather than the marked alteration in the orientation of blades in adjacent sheets typical of many Strophomenida (see Armstrong 1969). Again, a well-differentiated primary layer has not been discovered unequivocally. Recrystallization is most common at the shell surfaces and pressure solution of the enclosing sediments interferes with the external shell fabrics. However, over certain areas of the valve's exterior a layer of small laminae can be seen (Pl. 5, fig. 2). These are only 3–4 µm wide, appear to grade within one or two layers into the full-sized fibres, and probably constitute a remnant primary layer.

We have, therefore, within the Aegiromeninae a differentiation of at least the secondary shell layer away from the standard parallel fibrous fabric typical of geologically older plectambonitaceans (*Ahtiella*, *Inversella*, *Toquimia*, *Leptestia*, *Leptelloidea*, and *Bilobia*), genera studied to demonstrate the standard nature of the early plectambonitaceans (Pl. 5, figs. 3, 4) and which continued on within the Sowerbyellinae. *Ptychoglyptus* and *Xenambonites* have not been studied.

It is Havlíček's opinion (1969 : 38) that the sub-family Aegiromeninae is the group from which chonetaceans evolved. Further, he assumed '*Chonetoidea* to be incontestably the direct precursor of the superfamily Chonetacea in which canals extended posteriorly into long hollow spines'. Unfortunately it has been impossible to find *Chonetoidea* specimens suitably preserved for the study of their shell, but morphological considerations support Havlíček's opinion that *Chonetoidea* evolved from a *Sericoidea*-like ancestor.

It is necessary, therefore, to test this suggested phylogeny against the shell structure of the oldest known chonetaceans. The oldest undoubted species is *Chonetes* (*Eochonetes*) *primigenius* Twenhofel (1914) from Anticosti Island, Canada. Twenhofel recorded the species from four formations, the Charleton (≡ Vauréal) and Ellis Bay Formations of Richmond (high Ordovician) age, and the Gun River and Jupiter River Formations of Lower Silurian age. The holotype was figured from the Gun River Formation and a ventral valve exterior figured from the Charleton (Vauréal) Formation. It is still generally agreed that the Ellis Bay Formation is uppermost Ordovician in age. Dr. O. A. Dixon has been kind enough to send rock samples with this species from Mile 5, Juniper River and Mile 2 47 Mile Road, Anticosti, from the Ellis Bay Formation. Amongst these are several examples of dorsal valve interiors (Pl. 5, figs 5–8), figured for the first time here, and the shell substance is reasonably well preserved in the ventral valves. The species was assigned by Muir-Wood (1962) to her new genus *Strophochonetes*. Boucot & Harper (1968) called into question the validity of both *Strophochonetes* and *Protochonetes* of Muir-Wood (1963). A study of Lindström's specimens of *Strophochonetes cingulatus* (in the BM(NH) collections and used by Muir-Wood in defining the genus) and of *Protochonetes ludloviensis* Muir-Wood, type species of that genus, together with specimens of *P. striatellus* (Dalman) from the Wenlock of Gotland, a species very close to *ludloviensis*, convinces me of the separate identity of the two genera. In the author's experience unabraded *S. cingulatus* and *S. primigenius* specimens always have a ventral median accentuated rib. The outline is relatively less wide than in *Protochonetes ludloviensis* or *P. striatellus*, and whilst spines may be abundant on *Strophochonetes* (up to at least seven pairs) they extend more or less perpendicularly from the valve margin. Those of *Protochonetes* extend posterolaterally. A divided ventral median septum in *Strophochonetes* has never been observed.

It is perhaps significant that a collection, as yet undescribed, made by Dr. Cocks from the low Wenlock Knockgardner Beds of Girvan, Scotland, includes many chonetacean specimens which appear to show characteristics intermediate between those of the types of *Strophochonetes* and *Protochonetes*. The specimens are small, approximately 10 mm. wide, and in outline resemble *Protochonetes*; the ribbing is even but the ventral median septum is ill defined posteriorly. Spines seem to be variably disposed, some nearly perpendicular, others at an angle to the hinge line.

Chonetacea

The shell of *S. primigenius* is characterized by its parallel to subparallel arrangement of fibre-like elements (Pl. 6, fig. 1, 2) which both overlap adjacent fibres laterally and, in other parts of the shell, abut to their neighbouring fibres with a more or less perpendicular plane of separation. Whilst the packing of these fibres is tight, they retain a discreteness and do not show signs of having fused laterally with adjacent units, as is the situation in the bladed and sheet fabrics of Armstrong (1969) or truly laminar fabrics of Williams (1968, 1970). These lath-like fibres are 6 to 10 μm wide and of variable thickness, but commonly between 2 and 4 μm thick. Pseudopunctae are sparsely developed in ventral valves (Pl. 6, fig. 1), but judging from the dorsal valve internal tuberculation pseudopunctae are more common in this valve.

A clearly differentiated primary layer has not been recognized, but towards the exterior of the valves the fibres have the appearance of Williams' 'crested lamellae' (1968 Pl. 21, figs 2, 4). In *Strophochonetes* this structure may result from slight recrystalization of the outermost shell layers.

The seemingly separate nature of the shell 'fibres' and lack of sheet fabrics leads to the conclusion that the shell was laid down essentially in the standard way as proposed by Williams (1956, 1968), that is by individual outer epithelial cells secreting the calcite for individual fibres which were separated from one another by organic sheaths.

Other chonetacean records from Ordovician rocks are unsatisfactory. Study of the specimens recently referred to by Lister, Cocks & Rushton (1970) from upper Ordovician rocks of the Bobbing Bore, Kent indicates that they probably are chonetaceans. However, preservation is poor and the shell material is lacking or altered. Reed (1944) described a new species, *Chonetes* (*Eochonetes*) *celtica*, from the Upper Ordovician Balclatchie Beds of Ayrshire, Scotland, which was assigned to *Strophochonetes* by Muir-Wood (1962). Neither spines nor spine bases can be seen on the holotype in the Hunterian Museum, Glasgow and the acutely angular relationship of the interareas is much more suggestive of a plectambonitacean than a chonetacean.

From Middle Llandovery rocks of Newlands, Girvan, Scotland Dr. Cocks has found two ventral valves of a *Strophochonetes* species showing spines, but no shell is preserved. By mid-Silurian times chonetaceans were becoming more abundant, but their main diversification did not take place until the Upper Palaeozoic during which first the Plectambonitacea and then the Strophomenacea died out.

In addition to *Strophochonetes* the following chonetaceans have been studied for shell structure: *Protochonetes striatellus* (Dalman) from the mid Silurian of Gotland, from where also comes a small chonetacean species, possibly *Eoplicanoplia* Boucot & Harper 1968; *P. ludloviensis* Muir-Wood from Upper Ludlow rocks of Eastnor, Hertfordshire; *Dawsonelloides canadensis* (Billings) from Lower Devonian rocks of Gaspé, Quebec; *Retichonetes vicinus* (Castelnau) from mid-Devonian Arkona shale of Ontario; *Rugosochonetes* species from Lower Carboniferous strata of County Fermanagh, N. Ireland; Mississippian of Oklahoma, and basal Namurian of Northumberland; *Neochonetes* from the Permian of Texas, USA, and specimens from the Permian of Russia.

In general the shell fabric of these later chonetaceans supports that seen in *S. primigenius*. Pseudopunctation, including well differentiated taleolae, became more strongly developed by the lower Devonian (Pl. 7, figs. 1, 3) and continued within the stock. The greater part of the shell thickness retained a lath-like fibrous nature (Pl. 7, figs 1, 2), although each 'fibre' was only from 2–4 μm wide and up to about 1μm thick, until the early Devonian when there are clear signs of lateral fusion of 'fibres' (Pl. 7, fig. 3) into units 8–10 μm wide. In lower Carboniferous specimens, such as *R. silleesi* Brunton, while lath-like units are readily distinguishable throughout much of the shell their orientation from layer to layer is variable (Pl. 7, fig. 4) and towards external surfaces sheets of blades are developed (Pl. 8, figs 1, 2) into what approaches a true cross-bladed fabric (Pl. 8, fig. 3).

Thus it seems that a trend away from the typical fibrous secondary shell of many Ordovician Plectambonitacea can be traced through members of the Aegiromeninae into the earliest known chonetaceans of the Lower Palaeozoic and on into the Upper Palaeozoic when chonetaceans were at their most abundant and diverse (Text-fig. 6). It seems, therefore, that within the Chonetacea the laminar shell fabric, like that of the Strophomenida other than the Plectambonitacea, developed independently from that in the Strophomenacea which, in Williams' (1970) view, arose from a Cambro-Ordovician plectambonitacean-like ancestor derived from the nisusiid Billingsellacea (Text-fig. 7). This change in shell structure involved a reduction in the size of fibres indicating a reduction in the size of the secretory outer epithelial cells. This trend continued in the early chonetaceans, along with a loss in regularity and consistency in growth direction of the fibres at any one time or at different times during ontogeny. This may have resulted from the increased development of pseudopunctæ to which small areas of specialized epithelium became fixed. In this way local areas of epithelium may have been retarded in their general anterior growth, so distorting the uniformity of calcite secretion in adjacent areas. Furthermore, an increasingly mobile epithelium, in terms of periodic retraction from the valve edges, would have resulted in the likelihood of renewed forward growth taking place in slightly altered directions and consequently the non-alignment of new fibres.

If the development of all laminar shell is as inferred by Williams (1968) for *Juresania* then a continued reduction in epithelial cell size did not continue. In Williams' view a single epithelial cell (implied by his text-fig. 25 as being about 12 μm wide) secreted several blades, each to some extent separated by impersistent proteinous strands and abutting laterally to form more or less continuous sheets. The alternative is for each blade to have been secreted from single epithelial cells, in the case of Devonian and Carboniferous chonetaceans between 2 and 5 μm wide, which progressively ceased to produce the protein sheets which separate normal fibres. But in whatever way laminar shell was deposited it is clear that the epithelium was unusually mobile by modern standards (Brunton 1969), and that the proteinous strands and old cell boundaries were ruptured at times of mantle regression. At such times the regressing epithelial cells probably laid down a proteinous sheet continuous with the periostracum. During transgressive renewed

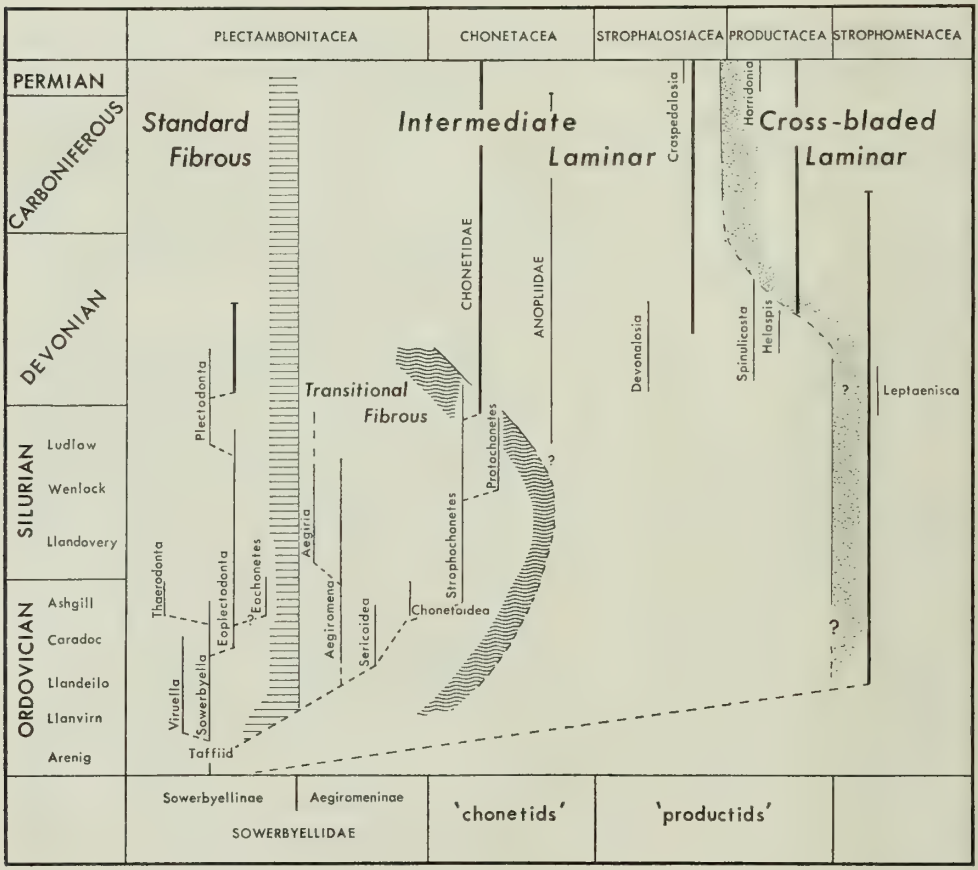

FIG. 6. Inferred phylogenetic relationships between those genera of the Plectambonitacea and Chonetacea in which shell microstructure has been studied. Those taxa in which the name is horizontal have not been studied in detail. Principal features of the secondary layer shell fabric are differentiated and labelled in italic script. Five productid genera are included to indicate the results of preliminary investigations on their shell structure and relationships. It is suggested that the plectambonitacean to chonetacean changes in shell structure may have continued and given rise to the productids. *Leptaenisca*, commonly cited as ancestral to the Productacea, would seem not to have a typically strophomenacean shell of cross-bladed laminae.

calcite deposition these proteinous layers would have become entombed within the shell fabric and consequently separated one skeletal sheet from another so accentuating the lamination typical of this type of brachiopod shell fabric.

Preliminary results from the investigation of mid-Devonian productacean and strophalosiacean shell microstructures shows them to be composed of semi-parallel lath-like units 2–3 μm wide with little development of laminar sheets (Pl. 8, fig. 4, Pl. 9, fig. 1), whilst Carboniferous and Permian productaceans have typical cross-bladed fabrics (Pl. 9, figs 2–4). Such fabrics may be explained as a continuation of the evolutionary trend outlined above, but further study is in progress on this

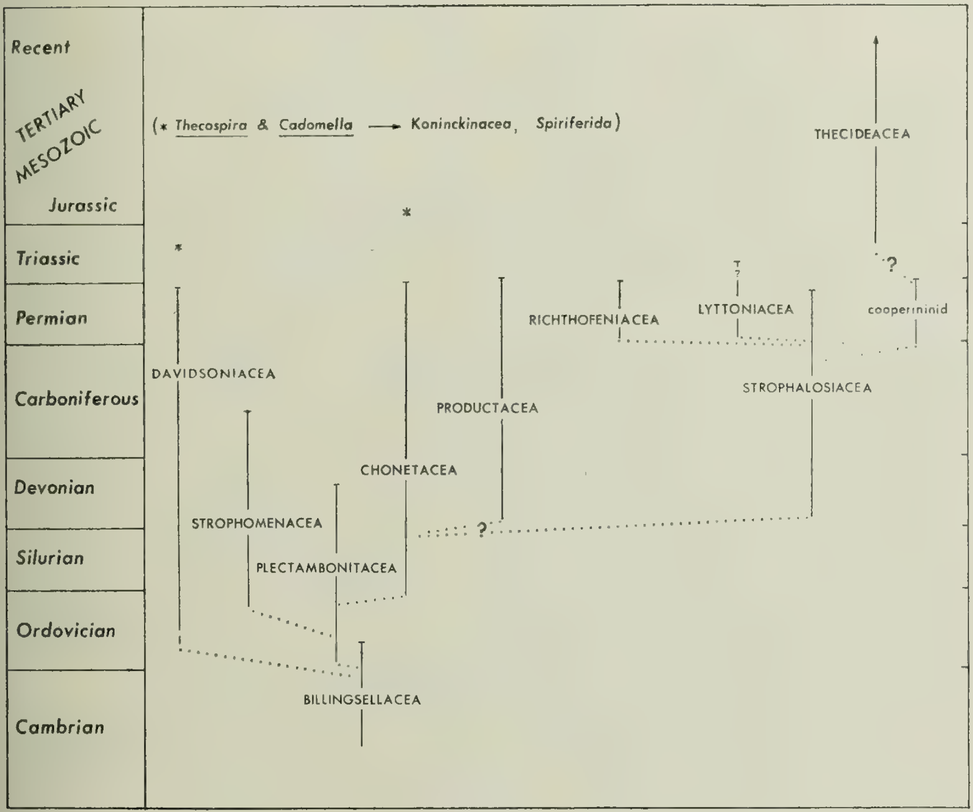
Recent
TERTIARY
MESOZOIC
Jurassic
Triassic
Permian
Carboniferous
Devonian
Silurian
Ordovician
Cambrian
(* Thecospira & Cadomella → Koninckinacea, Spiriferida)
THECIDEACEA
*
*
?
RICHTHOFENIACEA
LYTTONIACEA
?
cooperininid
DAVIDSONIACEA
STROPHALOSIACEA
PRODUCTACEA
CHONETACEA
?
STROPHOMENACEA
PLECTAMBONITACEA
BILLINGSELLACEA

FIG. 7. Speculative phylogeny of certain superfamilies of the Strophomenida, together with their ancestral stock, the Billingsellacea. The strophalosiacean *Cooperina*-like group may be close to the stock from which the Thecideacea arose. Pseudopunctation was developed within the Davidsoniacea and at the start of the Plectambonitacea. Endopunctation developed in the Thecideacea, possibly early in the Jurassic. (**Thecospira* and *Cadomella* have been placed in the Davidsoniacea and Chonetacea respectively. It is thought likely that they belong to the spiriferide Koninckinacea).

question and the more traditional derivation of these stocks, via *Leptaenisca*, from the Strophomenacea may yet prove possible. Study of two imperfectly preserved specimens from the Haragan Shale of Oklahoma shows that the shell fabric of *Leptaenisca* is not truly laminar. The genus can not, therefore, be excluded from possible productidine ancestral stocks by reason of its shell alone. The shell of Permian strophalosiaceans appear to have retained a less laminar shell than productaceans.

VI. DISCUSSION AND CONCLUSIONS

This study, based upon shell microstructure, supports Havlíček's conclusions, based upon morphology and stratigraphy, that the family Chonetacea was derived from aegiromeninid Plectambonitacea.

Ordovician plectambonitaceans have a shell structure with small 'fibres' (possibly equivalent to the 'laminae' of Williams 1968) about 6 μm wide in the outer layer, which grade rapidly into a normal parallel-fibrous shell fabric similar to that of Recent brachiopods. This gradational change may simply be a reflection of the increase in size of epithelial cells away from the mantle edges; a possibility which cannot be tested without studying well preserved and undamaged shell margins. Within the mid-Ordovician to Silurian aegiromeninid Plectambonitacea a progressive change occurred which links the shell structure of this subfamily to that of the earliest known chonetaceans in the uppermost Ordovician.

Like some aegiromeninids, the lower Palaeozoic chonetaceans have a shell composed of small lath-like fibres which retain their individuality, in contrast to the sheet structures that began to develop in Upper Palaeozoic specimens.

The internal morphology of aegiromeninids, particularly that of the dorsal valve, is simpler than that of most other plectambonitaceans. Within the subfamily various morphological features were 'tried', some of which may be homologous to chonetacean characteristics, and Havlíček (1967) suggested that some genera altered their way of life from benthonic to epiplanktonic, being attached to floating algae. Thus it was a group undergoing much evolutionary change.

The socket ridges of Sowerbyellinae extend antero-laterally and probably assisted in the support of the body wall. In the Aegiromeninae socket ridges are commonly reduced, whilst in the Chonetacea they functioned only as socket bounding ridges and the role of body-wall support was filled by the anderidia. The anderidia probably developed from the outer side septa of the Sowerbyellinae and the low ridges dividing the dorsal adductor muscle scars of, for example, *Aegiromena*. An anteriorly prominent dorsal median septum is common to Aegiromeninae and Chonetacea and in both taxa it is believed to have been involved in the support of a simple schizolophe, more or less fused to the dorsal mantle. From the Sowerbyellinae, through the Aegiromeninae and into the Chonetacea there is a reduction in the skeletal support for the teeth. Dental plates are reduced and all but lost in *Sericoidea*, *Sentolunia* and *Chonetoidea* and are lacking in the Chonetacea. In the ventral interareas of the last two genera Havlíček (1967) has recorded fine canals penetrating the shell substance, as in contemporaneous *Eochonetes*, and these structures are essentially the same as the canals leading from the valve interior into the spines of chonetaceans. All that is required is for the plectambonitacean epithelial evaginations, responsible for the canals, to have retained generative buds at their tips so as to have grown posteriorly beyond the posterior margin. Being generative, in the same way as the rest of the mantle margins, implies the sequential secretion of a protective periostracum followed by mineral deposition around the epithelial cells to form a hollow spine. It is rather as if the epithelial cells of an endopunctum retained a generative tip so that growth, restricted to that local area, continued more or less perpendicular to the valve surface. (This is not to say that I believe in a direct relationship between endopunctae and spines.)

The weakly concavo-convex profile, the outline and external ornamentation of *Sentolunia* and *Chonetoidea* are in accord with the morphology of the first chonetaceans, *Strophochonetes*, and it may be that the strong ventral median rib characteristic of this genus (Pl. 6, figs. 3, 4) is a remnant feature of the Plectambonitacea. In contrast to Boucot & Harper (1968) the present study indicates that *Protochonetes* evolved from *Strophochonetes*. Shell structure studies on the Anopliidae suggest that their origin was in common with other chonetaceans and that this family evolved in the lower to mid-Silurian by morphological differentiation.

In considering the distribution of ancestral stocks and general evolution of the chonetaceans it should be remembered that the present wide geographical separation between the European *Chonetoidea*-like stock and North American *Strophochonetes* would have been less in Upper Ordovician times, if current theories of continental drift and the degree of crustal shortening in the North Atlantic region during the Caledonian orogeny are accepted. In discussing Ordovician faunal provinces Williams (1969) suggested a Caradocian palaeogeography in which oceanic currents would have distributed marine organisms (other factors permitting) in the European and North American provinces. Within the Ashgill of Bohemia, Havlíček (1967) and Havlíček & Vaněk (1966) record several aegiromeninid species morphologically close to the chonetacean ancestor, but no chonetaceans. In the Richmond Series of Anticosti Island, Canada, Twenhofel (1914) only recorded *Plectambonites sericeus* (presumably *Sowerbyella*) with *Chonetes primigenius*. Thus, unless more recent faunal work on Anticosti proves the presence of Aegiromeninae in rocks older than those from which the first *Strophochonetes* are recorded it seems this was not the area in which the evolutionary change took place. Both Aegiromeninae and Chonetacea are found in Girvan, Ayrshire, but the Chonetacea postdate those at Anticosti. It seems possible, therefore, that the evolutionary change took place in the Upper Ordovician within the southern region of Williams' palaeogeographical model.

Using Williams' (1969) model it is suggested that some Bohemian Aegiromeninae, possibly *Chonetoidea* itself, became widely distributed along the southeast margin of the Caradocian seas, perhaps helped by having become epiplanktonic through their ability to fix to marine algae (Bergström 1968). Within this stock posterior 'hold fasts' retained the ability to secrete shell material, so evolving tissue-filled posteriorly directed spines. Like their ancestors the spat would have been attached by their pedicle to hard material on the sea-floor, or perhaps to seaweeds. However, at an early age the pedicle atrophied and the development of the spines would have helped stabilize benthonic specimens residing in areas subject to marine currents, particularly those specimens facing into the current which were consequently more susceptible to being overturned posteriorly when the shell opened. In a low velocity unidirectional flow from front to back a 'dead water' zone behind the raised dorsal valve might have prevented the burial or erosion of the spines spread out more or less at the sediment to water interface. These adaptations contributed to the evolution of the Chonetacea in the Lower Palaeozoic fine-grained sedimentary environments in which they are commonly found. During Upper Palaeozoic times chonetaceans spread into regions of coarse shelly detritus as well as living in silt and mud environments.

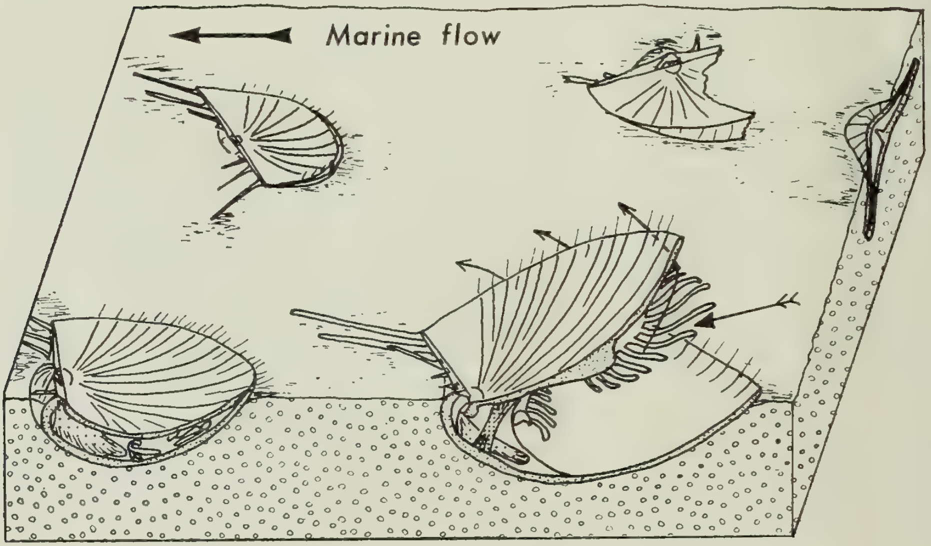

Fig. 8. Hypothetical chonetacean adult community on a soft-bottomed sea floor. The two shells at the top right are dead; one overturned (seen in transverse section), the other part buried. The other three specimens are living (with marginal setae). The two front specimens are cut in longitudinal section; on the left parallel to and on the right along the median line. In these specimens musculature, body wall and lophophore are represented and the arrows indicate the possible flow of water within the brachial cavity.

The spread of chonetaceans to Britain and Europe would have been achieved by Williams' northeasterly oceanic flow, together with the more general break-down in provinciality which started at the close of the Ordovician and became marked during the mid- and upper Silurian.

Representatives of the Chonetacea were the first brachiopods to have developed long tubular spines. Ontogenetic studies of Carboniferous species indicate that these spines normally grew posteriorly at the time of their origin. Thus, in relation to the commissural plane the lateral spines at any particular growth stage were directed posteriorly and were well suited for the support of shells on the substrate. If there was a directional water flow in the environment and if the young shell was able to choose its orientation on settlement it is likely that the water circulatory system outlined above would best have been served by facing into that flow. In this situation posteriorly directed spines are well adapted to the stabilization of the shell (Text-fig. 8).

This demonstration of a gradual change in the shell microstructure from certain Plectambonitacea species to Chonetacea species supports the contention of Williams & Wright (1967) and others that we have here an evolutionary sequence; one which ranges across a subordinal division of the classification in the Treatise. Furthermore, the greater complexity discovered within the skeletal fabrics of these strophomenids allows wider speculation upon phylogenetic relationships and the modification of the relationships suggested by Williams in 1968 and 1970. The phylogenies of the superfamilies presented here (Text-fig. 7) are poorly understood at the points of origin of the Productacea and Thecideacea. Williams (1970) derived the Triplesiacea from the Davidsoniacea which arose from the Billingsellidae. In his view the nisusiid Billingsellacea gave rise to the Orthacea, Clitambonitacea, Gonambonitacea, Strophomenacea and Plectambonitacea.

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Locality details of figured specimens.

PLECTAMBONITACEA

Leptestia musculosa Bekker, Uhaku (C_{1c}) [Upper Llandeilo] Lower Ordovician of Uhaku, Estonia	Plate 5
Leptelloides leptelloides (Bekker), Kukruse (C_{11}) [Low Caradoc] Upper Ordovician of Kuttejou, Estonia	Plate 5
Sowerbyella (*Viruella*) *liliifera* Öpik, Kukruse (C_{11}) [Low Caradoc] Upper Ordovician of Estonia	Plate 2
Eoplectodonta transversalis (Wahlenberg). Lower Visby Marl, Llandovery, Lower Silurian of Nyhamn, Gotland, Sweden	Plates 1–3
Aegiromena aquila (Barrande), Zahorany Formation [Mid-Caradoc] Upper Ordovician of central Bohemia	Plates, 3, 4
Aegiria grayi (Davidson), Upper Wenlock, Silurian, of Dudley, Worcestershire, England	Plate 4
Sericoidea restricta (Hadding), high Ardwell Group [Upper Caradoc] Upper Ordovician of Craighead, Girvan, Scotland	Plates 4, 5

CHONETACEA

Strophochonetes primigenius (Twenhofel), Ellis Bay Formation [Ashgill] Upper Ordovician of Mile 5, Jupiter River and Mile 2, 47 Mile Road, Anticosti Island, Canada. (Mile 2 locality is 15–20′ above the base of the Ellis Bay Formation: Mile 5 is close to the top junction of the Ellis Bay Formation with the Becscie.) – *in lit.* TE Bolton, Geological Survey of Canada, Ottawa)	Plates 5, 6
Dawsonelloides canadensis (Billings), Grande Grève Limestone, Siegenian, Lower Devonian of Gaspé, Quebec, Canada	Plate 7
Retichonetes vicinus (Castelnau), Arkona Shale, Hamilton Group. Mid Devonian, ½ ml. upstream from Hungry Hollow Br., 2 ml. E of Arkona, Ontario, Canada	Plates 1, 7
Rugosochonetes silleesi Brunton, high Glencar Limestone, Low D zone Viséan, Lower Carboniferous, of Sillees R, nr. Bunnahone Lough, 2 ml. NW of Derrygonnelly, Co. Fermanagh, N. Ireland	Plates 7, 8

STROPHALOSIACEA

Devonalosia wrightorum Muir-Wood & Cooper, Lower Ferron Point shale, Hamilton Group, Mid-Devonian of abandoned Alpena Portland Cement Co. pit, Alpena, Michigan, USA	Plate 8

PRODUCTACEA

Helaspis luma Imbrie, Genshaw Formation, Hamilton Group, Mid-Devonian of Long Lake, 7½ ml. NNE of Alpena, Michigan, USA	Plate 9
Eomarginifera lobata (J. de C. Sowerby), Great Limestone, E_2 Lower Namurian of Greenleighton, Northumberland, England	Plate 9
'*Dictyoclostus*' sp, Carwood, Lower Mississippian of 2 ml. SW of Borden, Indiana, USA	Plate 9
Horridonia horrida (J. Sowerby), Lower Zechstein, Permian of Trebnitz, Gera, Germany	Plate 9

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PLATE 1

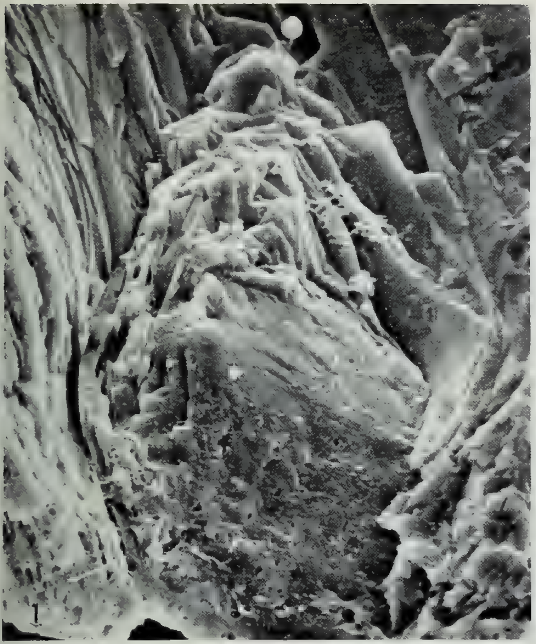
Pseudopunctae

FIG. 1. Fracture through a pseudopunctum, with taleola, close to the anterior margin of the dorsal valve of ***Rugosochonetes silleesi*** Brunton, from Viséan shales of Co. Fermanagh, N. Ireland. Eroded internal surface is to the bottom, viewed posteriorly. SEM (Scanning electron microscope), ×1150.

FIG. 2. Deeply exfoliated dorsal valve exterior of ***Retichonetes vicinus*** (Castelnau) from the middle Devonian Arkona Shale of Ontario, Canada, showing ribbing and a taleola within a pseudopunctum. The exterior of the shell is uppermost and the anterior is to the top. SEM, ×440.

FIG. 3. Deeply exfoliated dorsal valve interior of ***Aegiromena aquila*** (Barrande) from the Caradoc of Czechoslovakia, showing a completely 'fibrous' pseudopunctum. The valve interior is to the top. SEM, ×1100.

FIG. 4. The internal mosaic surrounding a pseudopunctum of ***Eoplectodonta transversalis*** (Wahlenberg), from the Llandovery of Gotland, Sweden. The anterior margin of the valve is to the right. SEM, ×550.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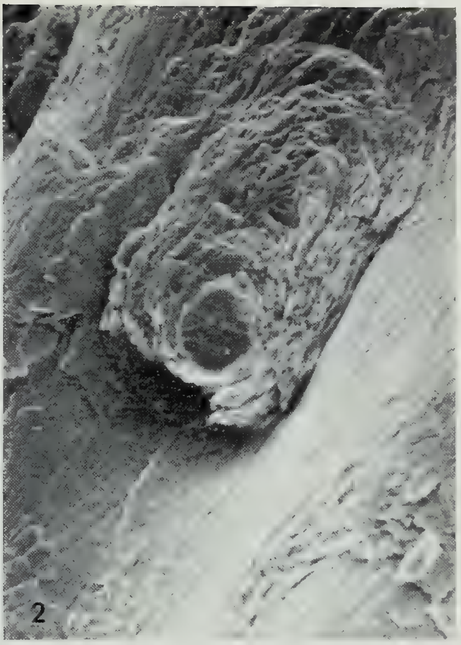
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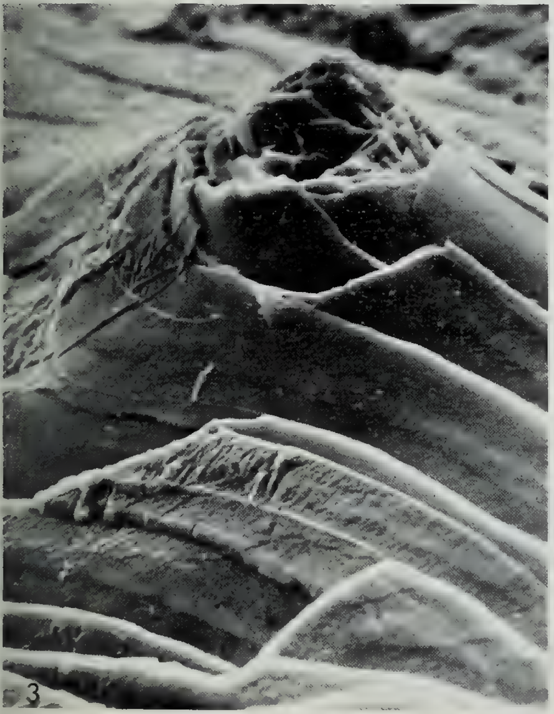
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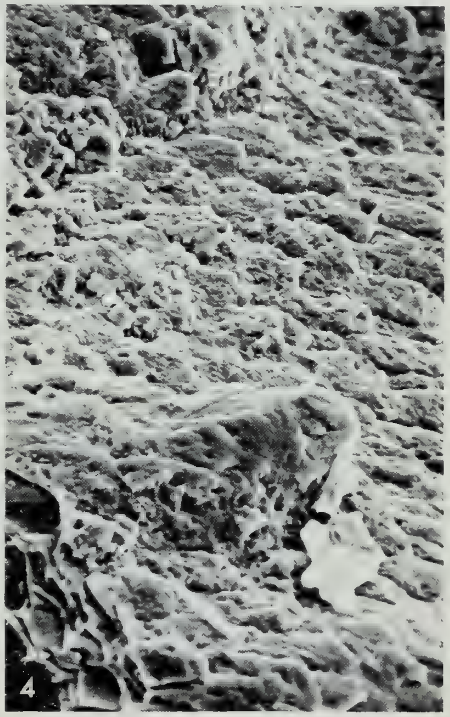
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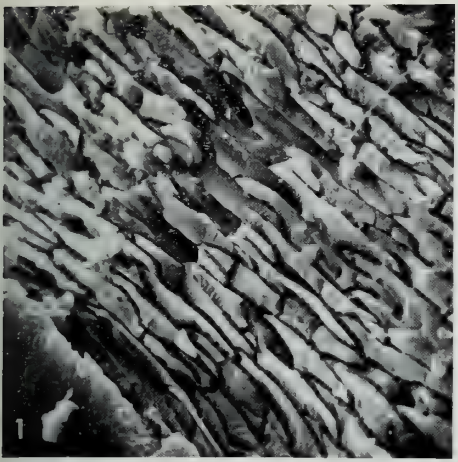
PLATE 2

Sowerbyellinae, standard shell fabric

Figs 1–3. ***Sowerbyella (Viruella) liliifera*** Öpik from Low Caradoc of Estonia. Valve interiors to the top. 1 – Cut and lightly etched transverse section of the ventral valve showing typical secondary fibres. SEM, × 1000. 2 – Fractured dorsal valve interior viewed posteriorly, showing the three dimensional aspect of typical secondary fibres. SEM, × 1000. 3 – Transverse fracture, close to dorsal valve margin, showing the transition from the sediment and primary shell, near the bottom, to secondary fibres at the top . SEM, × 1000.

Figs 4–6. ***Eoplectodonta transversalis*** (Wahlenberg) from the Llandovery of Gotland, Sweden. Valve interiors to the top. 4 – Latex impression of a ventral valve interior, i.e. an internal mould, showing the mantle canal impressions extending from deeply impressed lanceolate diductor muscle scars. × 3. 5 – Detail of the umbonal region of fig. 4 showing the small medianly placed adductor muscle scars. × 6. 6 – Transverse fracture through the external region of the valve showing, from bottom up, a thin layer of micrite, small lath-like primary lamellae and the start of standard secondary fibres. SEM, × 1200.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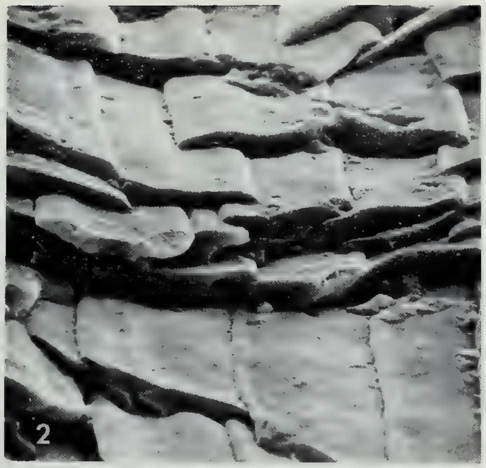
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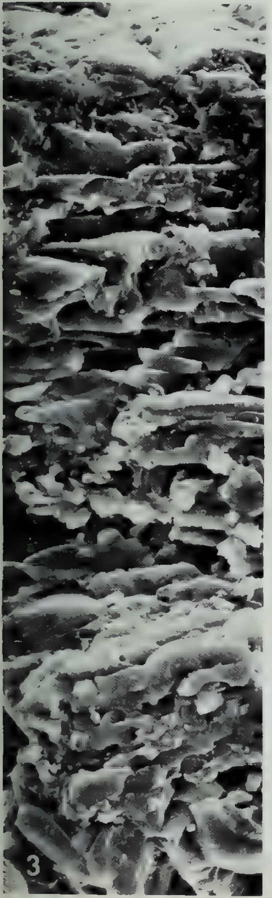
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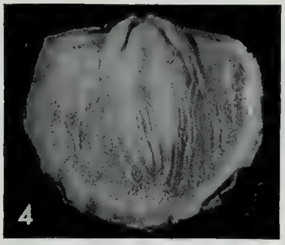
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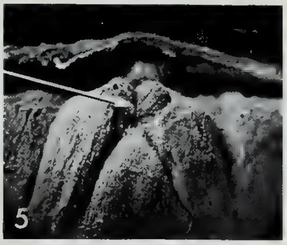
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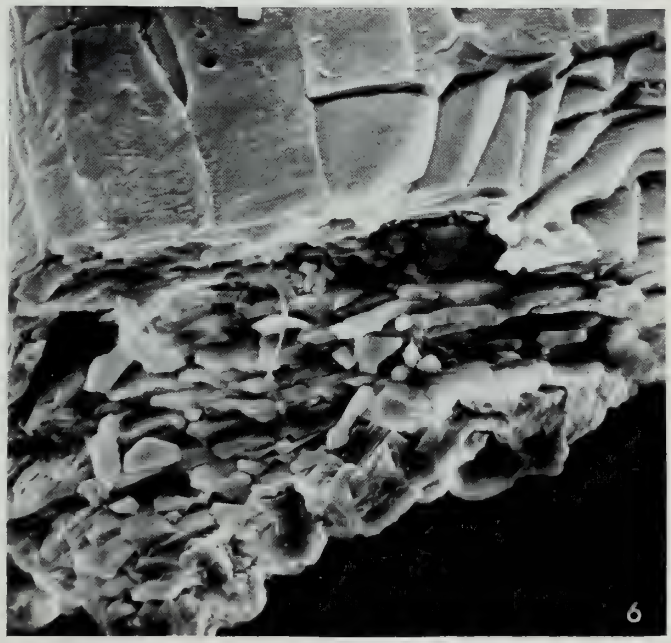
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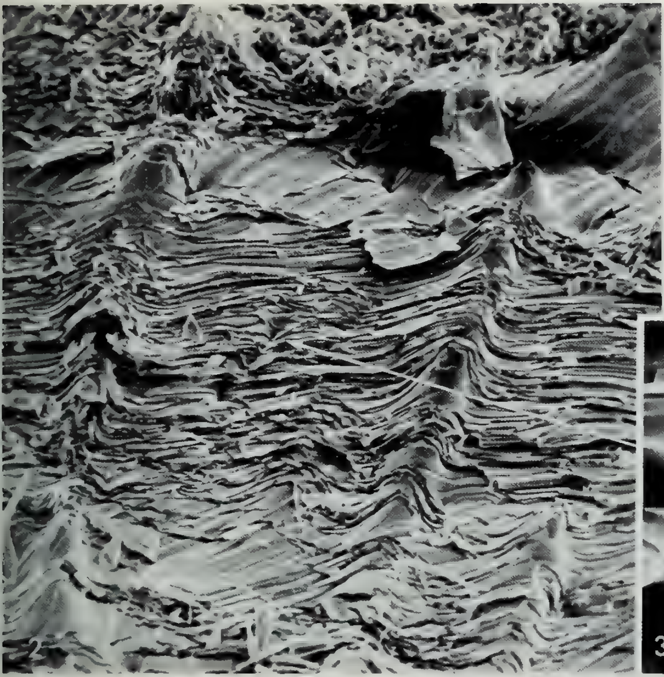
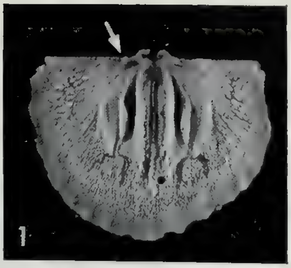
PLATE 3

Eoplectodonta and **Aegiromena**

FIGS 1 4. ***Eoplectodonta transversalis*** (Wahlenberg) from the Llandovery of Gotland, Sweden. Interior surfaces to the top. 1 – General view of the dorsal valve interior showing the prong-like elongations, despite broken tips, of the socket ridges. ×3. 2 – Exfoliated dorsal valve interior, about 1.5 mm. behind the anterior margin, showing pseudopunctae and several small endopunctum-like flexures of the secondary fibres (arrowed). SEM, ×250. 3 – Detail of endopunctum-like flexures, seen in section, from centre of fig. 2. SEM, ×3000. 4 – Detail of the internal surface, slightly exfoliated, showing the same flexures. SEM, ×1200.

FIG. 5. ***Aegiromena aquila*** (Barrande) from the Caradoc of Czechoslovakia. Deeply exfoliated dorsal valve interior (to the top right) near the antero-lateral margin and close to the external surface showing one of the rarely occurring almost typical secondary fibres. The antero-lateral margin is to the bottom. SEM, ×1200.

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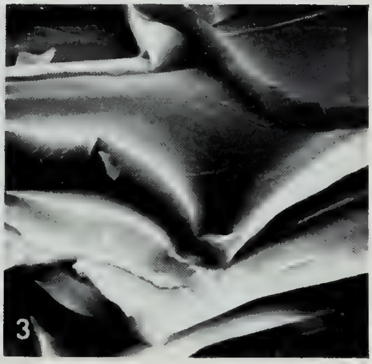
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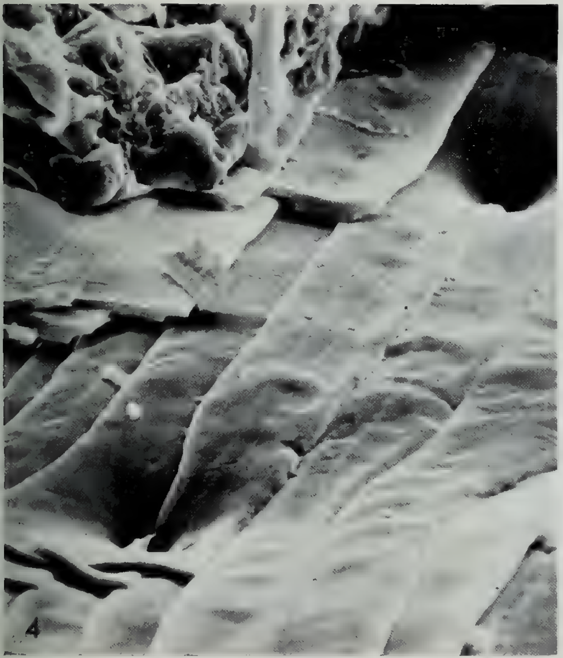
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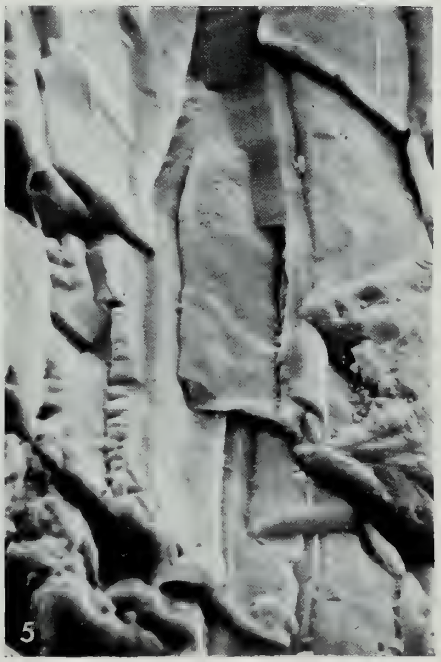
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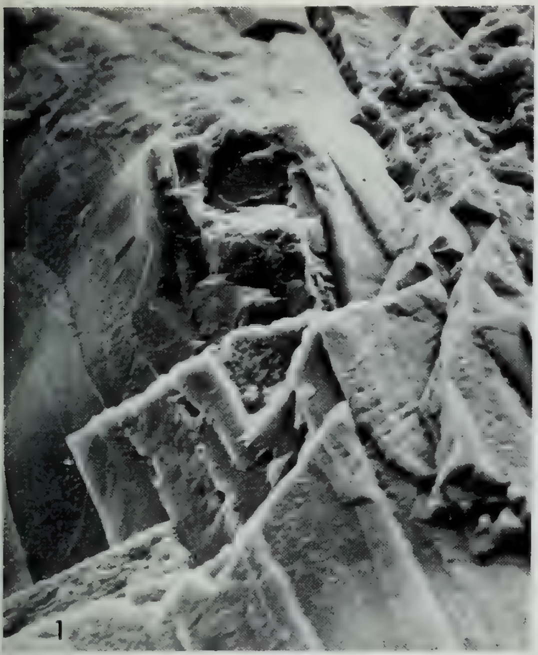
PLATE 4

Aegiromeninae

FIGS 1, 2. ***Aegiromena aquila*** (Barrande) from the Caradoc of Czechoslovakia. 1— Exfoliated dorsal valve, about half way through the shell and towards the antero-median margin, showing a pseudopunctum with taleola. Anterior is to the top. SEM, ×1100. 2 – Exfoliated ventral valve exterior showing ribbing, distribution of pseudopunctae, mainly within the rib interspaces, and parallel fibrous nature of the shell. Anterior is to the top. SEM, ×120.

FIG. 3. Deeply exfoliated ventral valve interior, close to the external surface, of ***Aegiria grayi*** (Davidson) from the mid-Silurian of Dudley, England, showing almost standard parallel fibres of the secondary layer. Interior is to the top left. SEM, ×1800.

FIG. 4. Exfoliated ventral valve exterior, near the antero-lateral margin, of ***Sericoidea restricta*** (Hadding) from the Caradoc of Girvan, Scotland, showing intermediate, atypical 'fibres'. Anterior is to the top. SEM, ×1000.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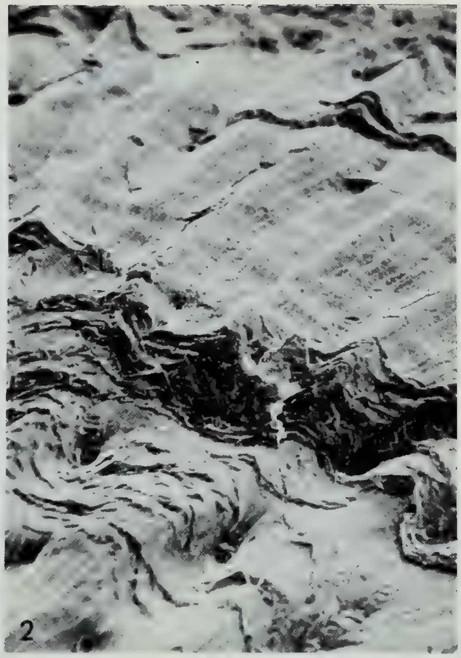
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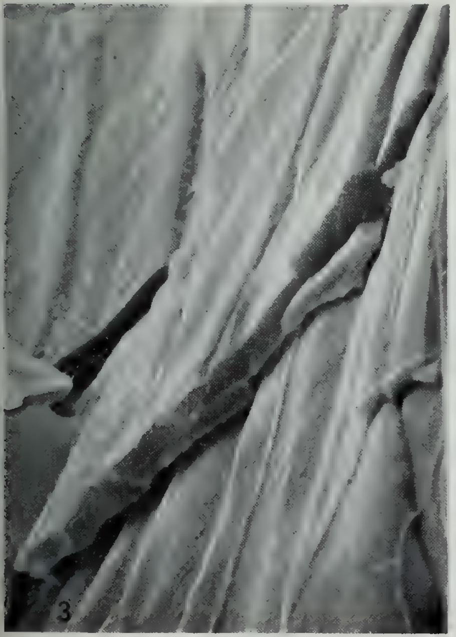
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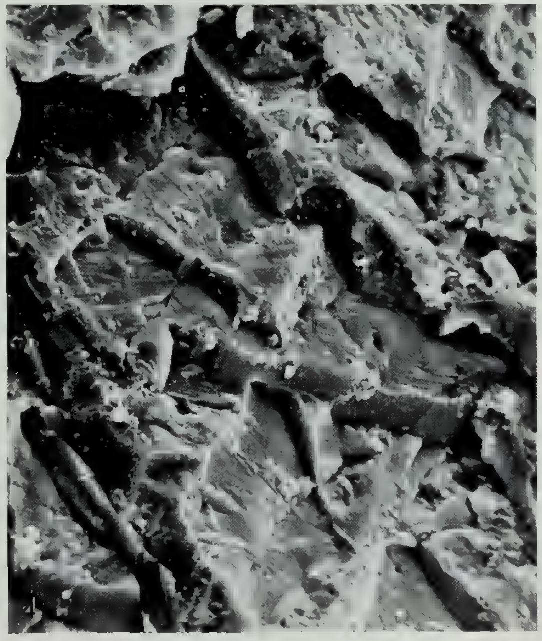
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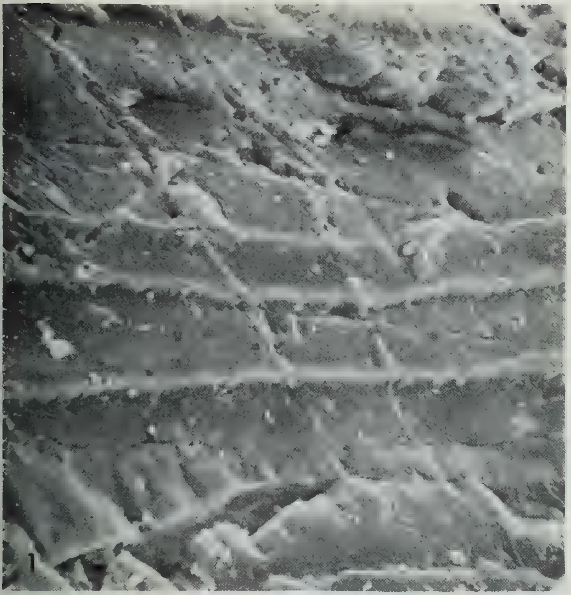
PLATE 5

FIGS 1, 2. ***Sericoidea restricta*** (Hadding) from the Caradoc of Girvan, Scotland. Exteriors to the top. 1 – Exfoliated ventral valve exterior showing subparallel 'fibres'. Antero-lateral margin to the left. SEM, × 1250. 2 – Slightly exfoliated ventral valve exterior close to its antero-median margin showing a single layer of small primary shell lamellae with subparallel 'fibres' below, including one near-normal transverse section (arrowed). Anterior is to the bottom. SEM, × 1000.

FIG. 3. Broken section near the anterior margin of the dorsal valve of ***Leptelloidea leptelloides*** (Bekker), from low Caradoc of Estonia, showing the typical secondary layer fibres of the non-aegiromeninid Plectambonitacea. Exterior to the top. SEM, × 1250.

FIG. 4. Deeply exfoliated ventral valve exterior, near the posterior margin, of ***Leptestia musculosa*** Bekker from the Upper Llandeilo of Estonia, showing typical secondary shell of the early Plectambonitacea. Interior uppermost. SEM, × 1000.

FIGS 5–8. ***Strophochonetes primigenius*** (Twenhofel) from the Ellis Bay Formation, Ashgill, of Anticosti Island, Canada. 5 – Interior of a young dorsal valve. × 4. 6 – Posterior view of a dorsal valve showing the quadrifid myophore of the cardinal process and low flanking chilidial plates (arrowed on one side). × 9. 7 – Ventral valve exterior and part of a dorsal valve interior. × 3. 8 – Detail of the dorsal valve cardinalia, note the strongly bilobed cardinal process. × 4.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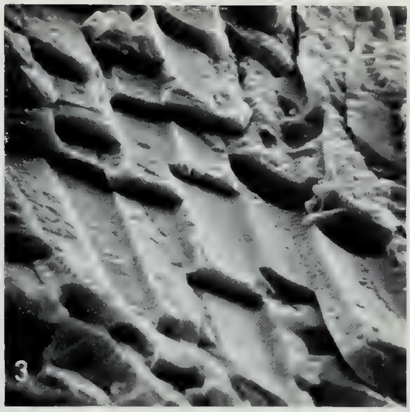
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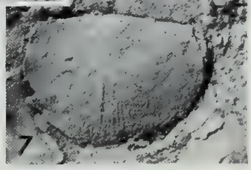
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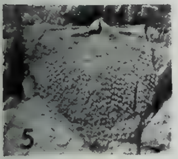
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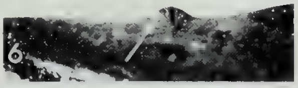
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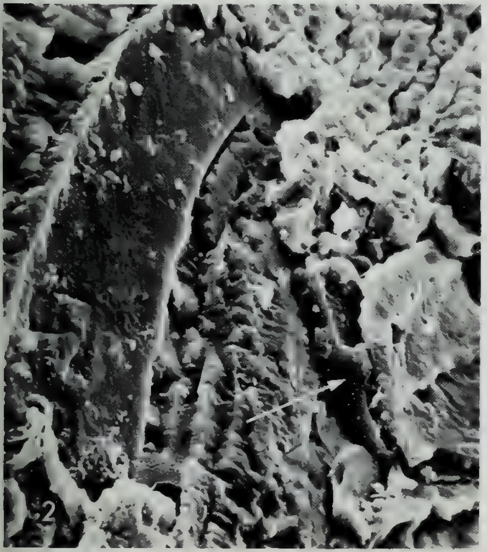
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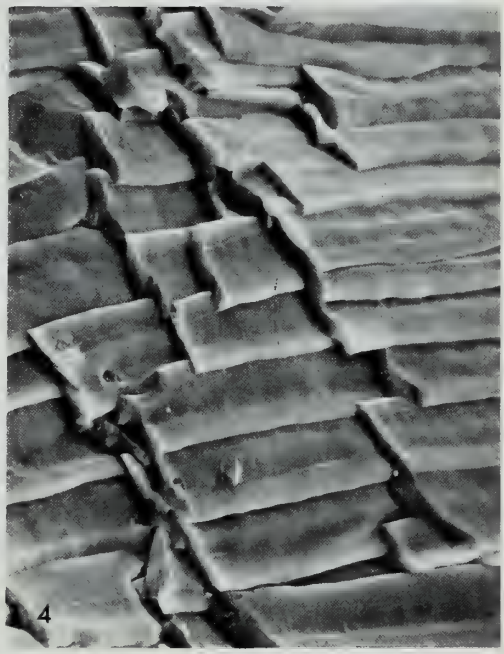
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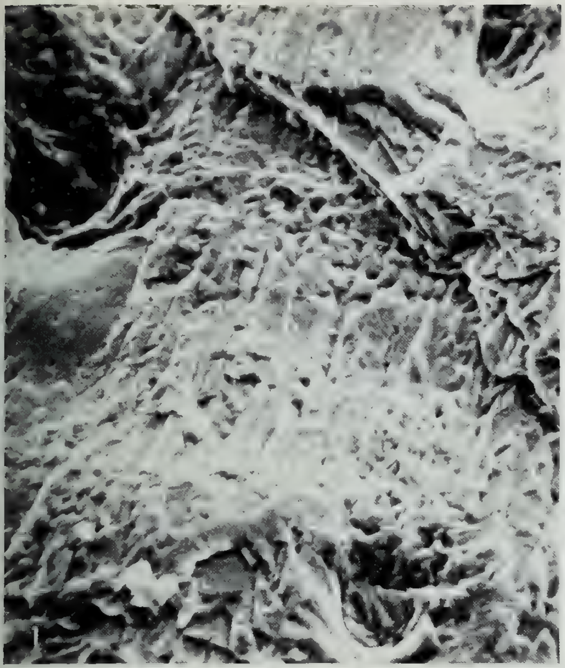
PLATE 6

Strophochonetes primigenius (Twenhofel)
from the Ellis Bay Formation of Anticosti Island, Canada.

FIGS 1, 2. Deeply exfoliated ventral valve exterior, close to the antero-lateral margin (to the top) showing pseudopunctae and the disposition of secondary transitional 'fibres'. SEMs, ×550 and ×1000.

FIG. 3. Well preserved ventral valve exterior showing the bases of spines and the accentuated median rib. ×3.

FIG. 4. Part of one of the fossiliferous slabs of limestone showing many ventral valve exteriors and one dorsal valve interior (figured Pl. 5, fig. 5). The accentuated median rib, typical of ***Strophochonetes*** and spine bases show on most specimens. × 2.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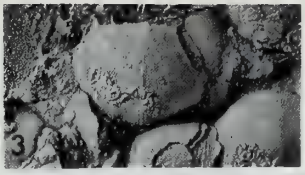
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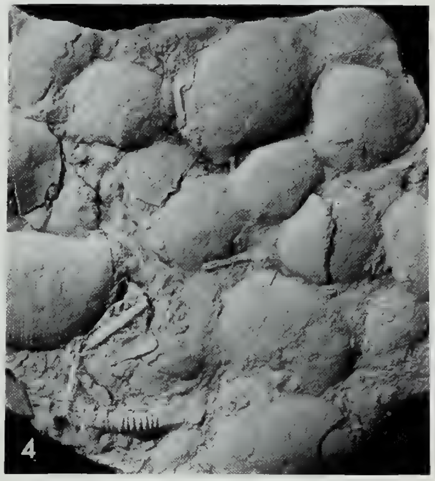
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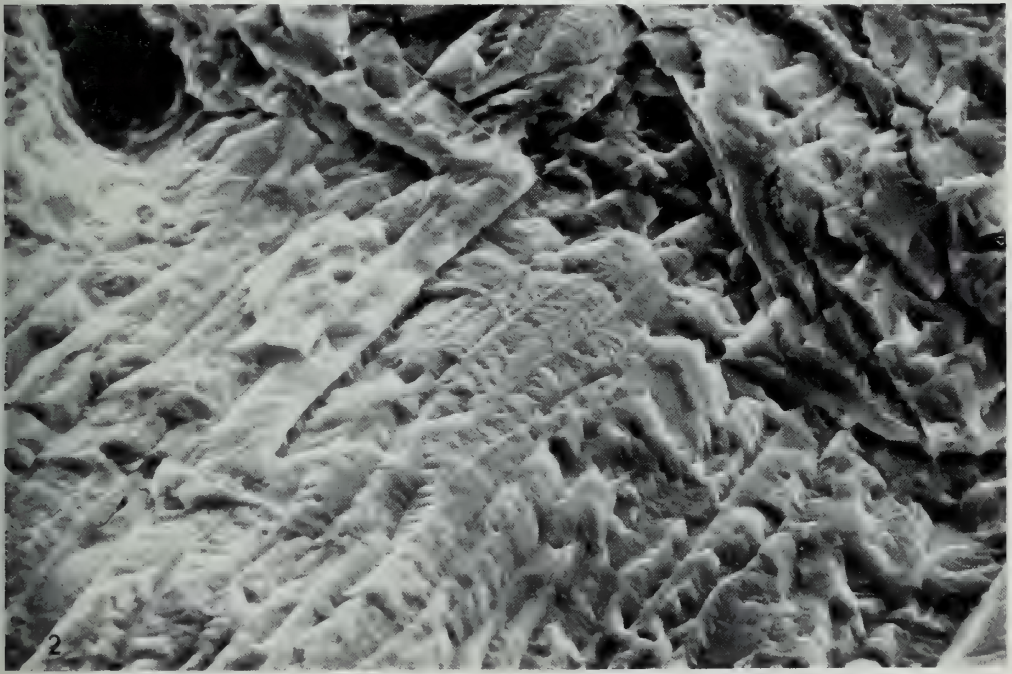
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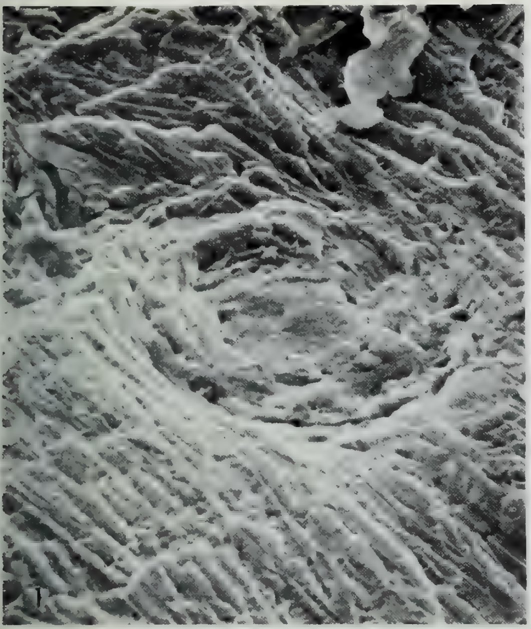
PLATE 7

Devonian and Lower Carboniferous Chonetacea

FIGS 1, 2. ***Dawsonelloides canadensis*** (Billings) from the Lower Devonian of Gaspé, Quebec, Canada. Valve exteriors uppermost. 1 – Deeply exfoliated exterior at a pseudopunctum with taleola. SEM, ×960. 2 – Small fibre-like units close to the external surface showing some lateral fusion. SEM, ×4000.

FIG. 3. ***Retichonetes vicinus*** (Castelnau) from the Mid-Devonian of Ontario, Canada. Slightly exfoliated ventral valve interior, at a pseudopunctum with taleola, showing the fusion of lath-like elements to give impersistent sheets. Antero-lateral margin to the bottom left. SEM, ×1100.

FIG. 4. ***Rugosochonetes silleesi*** Brunton from the Viséan of Co. Fermanagh, N. Ireland. Slightly exfoliated internal surface of a dorsal valve postero-medianly. Anterior is to the right. The individual shell lamellae are thin and do not retain a parallel orientation from layer to layer. SEM, ×2100.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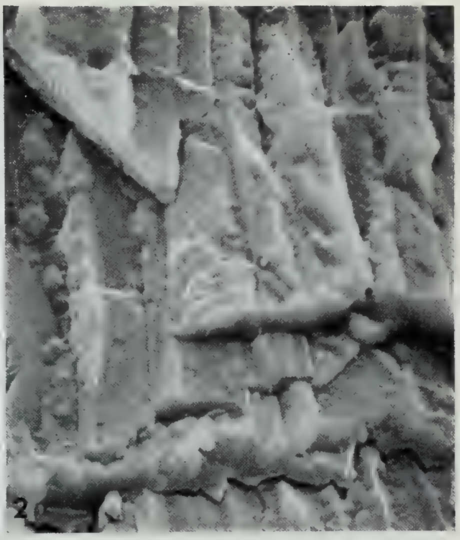
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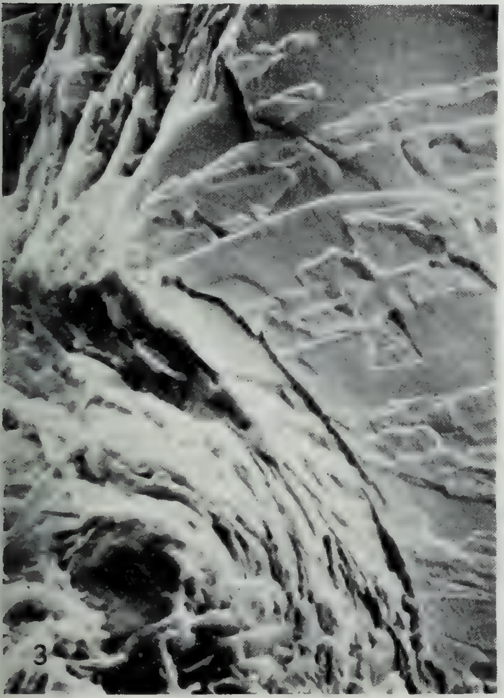
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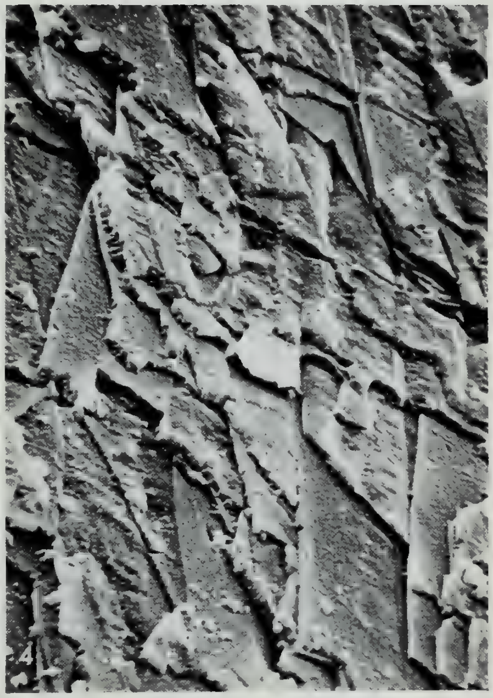
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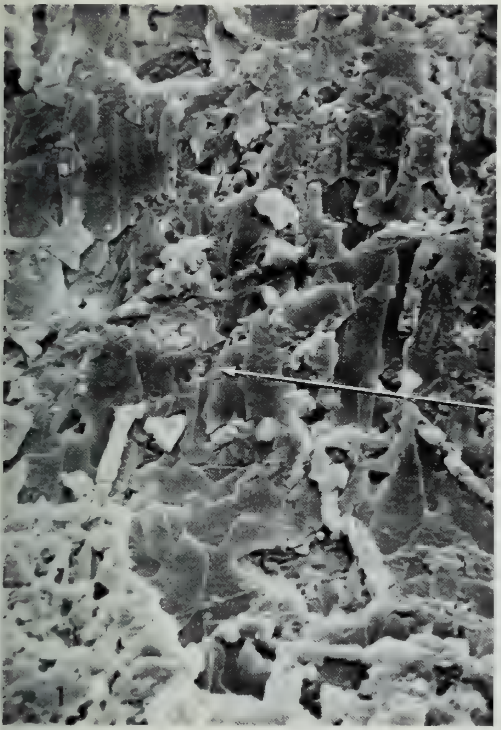
PLATE 8

FIGS 1–3. ***Rugosochonetes silleesi*** Brunton from the Viséan of Co. Fermanagh, N. Ireland. Dorsal valve exterior uppermost. 1 – Somewhat eroded external surface of the valve showing thin laminae forming wide sheets. SEM, ×1100. 2 – Detail from the centre of fig. 1 showing surfaces within the laminae like those onto which shell growth may have occurred in the living animal. SEM, ×5500. 3 – Fracture surface a little below the valve exterior (to the top) and close to the valve margin (to the bottom right) showing sheets of thin blade-like laminae. The sheet surface is broken by persistent and impersistent grooves which in life accommodated organic material separating individual blades. The ridges, at 20° to 30° from the grooves, mark the interblade boundaries of the adjacent removed sheet. SEM, ×2600.

FIG. 4. The strophalosiacean ***Devonalosia wrightorum*** Muir-Wood & Cooper, from the Mid Devonian of Michigan, U.S.A. Fracture surface near the anterior margin of the dorsal valve. The exterior is just off the top of the micrograph. Well-differentiated units resembling crested laminae.SEM, ×2200.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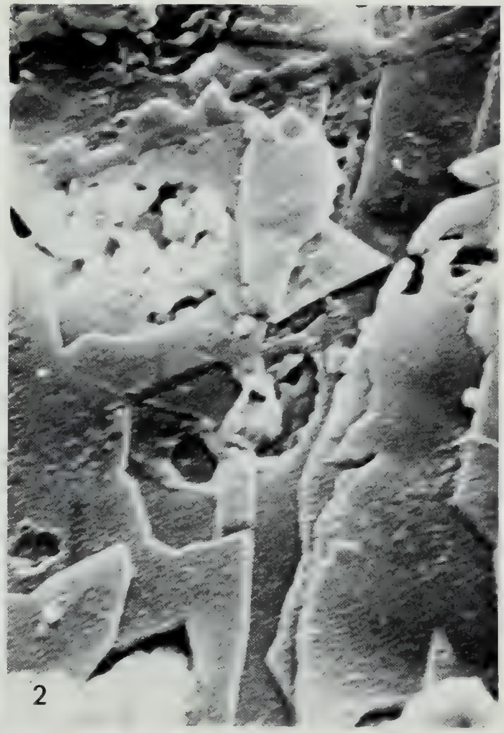
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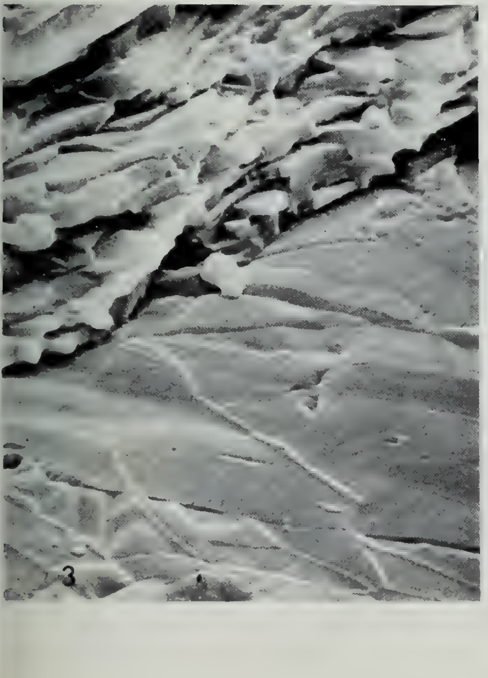
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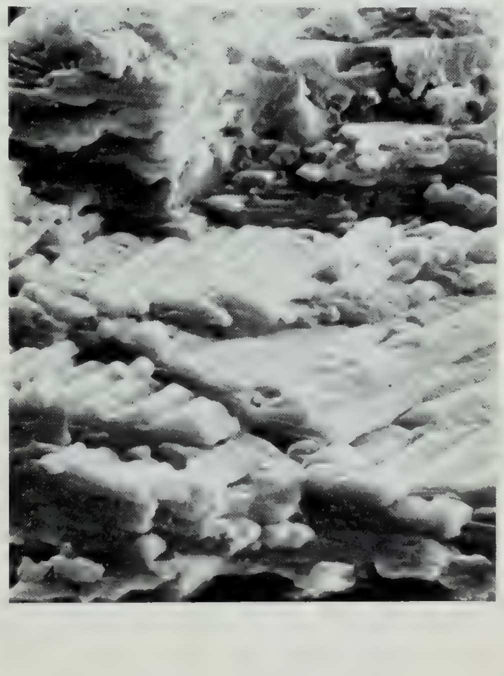


PLATE 9

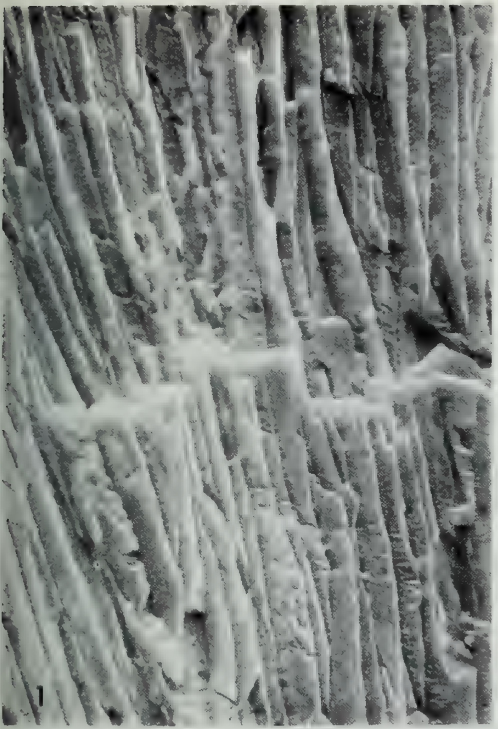
Productacea

FIG. 1. ***Helaspis luma*** Imbrie, from the Mid-Devonian of Michigan, U.S.A. showing external surfaces of crested laminae with subparallel orientation. SEM, × 2800.

FIG. 2. ***Eomarginifera lobata*** (J. de C Sowerby), from the Lower Namurian of Northumberland, England, showing cross-bladed structure near the centre of the base of the trail. Exterior to the top, anterior to the left. SEM, × 2000.

FIG. 3. **'*Dictyoclostus*'** sp. from the Low Mississippian of Indiana, U.S.A. showing cross-bladed fabric on an exfoliated interior from the ventral valve trail. SEM, × 4000.

FIG. 4. ***Horridonia horrida*** (J. Sowerby), from the Permian of Germany, showing typical cross-bladed fabric close to the external surface of the ventral valve near the postero-lateral margin. Exterior to the top right. SEM, × 4000.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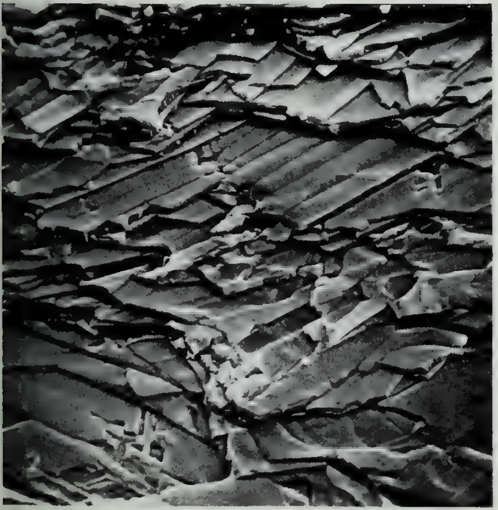
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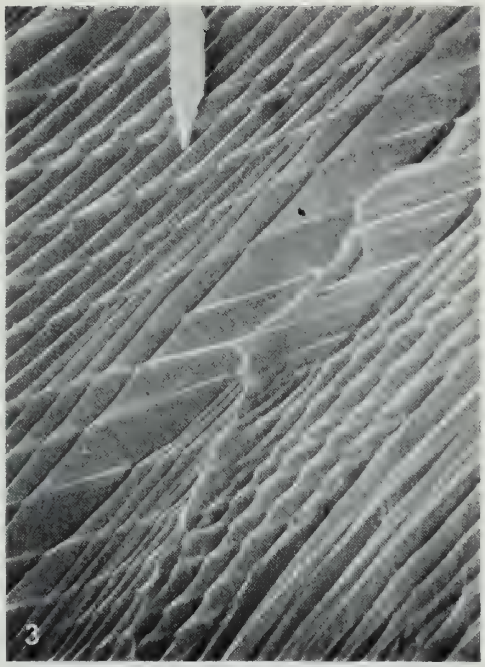
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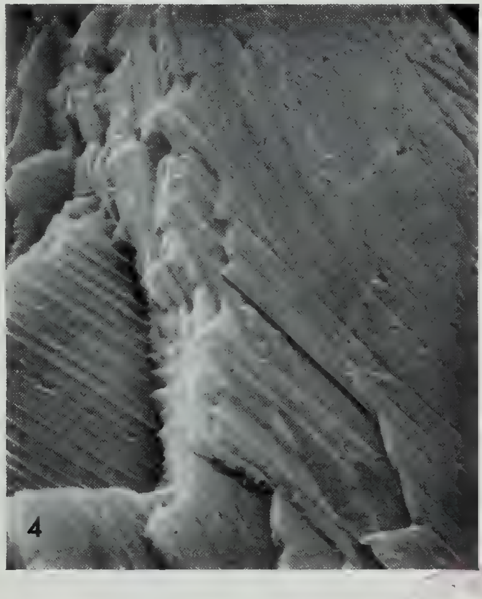
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POSTCANINE OCCLUSION IN CYNODONTS AND TRITYLODONTIDS

A. W. CROMPTON

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GEOLOGY Vol. 21 No. 2
LONDON : 1972

POSTCANINE OCCLUSION IN CYNODONTS AND TRITYLODONTIDS

BRITISH MUSEUM
30 JAN 1973
NATURAL HISTORY

BY

ALFRED WALTER CROMPTON
Museum of Comparative Zoology, Harvard University,
Cambridge, Mass.

Pp. 27–71; 7 *Plates,* 14 *Text-figures*

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POSTCANINE OCCLUSION IN CYNODONTS AND TRITYLODONTIDS

By A. W. CROMPTON

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SYNOPSIS

Within the gomphodont cynodonts and their descendants, the tritylodontids, it is possible to trace the initiation and progressive improvement of postcanine occlusion and complex masticatory movements, beginning with primitive cynodonts in which mastication did *not* involve actual contact between matching upper and lower postcanine teeth. Occlusion in advanced cynodonts was functionally similar to that of primitive mammals with tribosphenic molars, and the mechanisms by which occlusion evolved in the two groups also appear to have been similar. In primitive gomphodont cynodonts and primitive mammals the crowns of occluding teeth had to be moulded by wear to produce accurately matching shearing surfaces; major features of the crown were thereby obliterated. In advanced members of both groups the topography of the crowns was modified so that only a little wear was needed to produce matching shearing planes.

A clear correlation appears to have existed between the occlusal relationships of the teeth of cynodonts and their replacement patterns. The enamel of cynodonts and tritylodontids was thin and apparently worn through rapidly, so that the structure of the crowns was soon destroyed; in order to compensate for this, worn gomphodont teeth were lost from the front of the row and new ones added behind.

The tritylodontids were probably derived from traversodont cynodonts. The longitudinally orientated shearing planes on the postcanine teeth became more numerous and the relative extent of the backward movement of the lower jaw during the final stages of mastication was progressively increased.

Three new species of traversodont cynodonts are named (*Scalenodon hirschsoni, S. attridgei, S. charigi*).

INTRODUCTION

Accurate occlusion between cheek teeth with complex crown patterns is a mammalian character. It involves complicated relationships between the cusps, ridges and basins of occluding teeth and also mandibular movements that are seldom directly orthal during the final stages of the masticatory cycle (power stroke, Crompton & Hiiemae, 1969*a* & *b*), but are also partially transverse and forward. The relative amount of upward, forward and sideways movement during this phase of occlusion differs widely in the various mammalian orders. Many of the advanced cynodonts and tritylodontids independently developed occlusal patterns which in terms of function closely parallel those of later mammals. The purpose of this paper is to describe and discuss the development of postcanine occlusion in several groups of cynodonts, which are the most mammalian of the therapsid reptiles and the group from which mammals almost certainly arose. Although the cynodonts which had dental occlusion and which are discussed in this paper were not ancestral to mammals this study does throw some light on the mechanism involved in developing dental occlusion of the mammalian type.

Numerous authors have described and discussed the morphology of the teeth of therapsid reptiles; but few have described occlusal relationships, and except for one or two cases (Watson 1911, Parrington 1946) no attempt has been made to determine jaw movements during mastication or dynamic occlusion of the cheek teeth of this group. The functional aspects of mammalian occlusion also have been neglected, but recent papers on wear facets on the molars of living and extinct mammals (Butler, 1961; Mills, 1964, 1966, 1967; Kermack, Lees & Mussett, 1965; Crompton & Jenkins, 1967, 1968) and cineradiographic studies of mastication in a primitive mammal (Crompton & Hiiemäe, 1969, *a*, *b* & *c*) have provided a model with which to compare the dynamic occlusal relationships and possible jaw movements in cynodonts.

The infraorder Cynodontia (Fig. 1) arose in the late Permian, reached its greatest diversity in the Middle Trias and became extinct in the early part of the Late Trias. As will be shown below, the Tritylodontidae which survived until the Middle Jurassic can be considered as late survivors of the cynodonts. The Ictidosauria (*Diarthrognathus*, *Pachygenelus* and *Trithelodon*) were probably also late survivors of the Cynodontia and a case can perhaps be made for including them within the cynodonts. The cynodonts are usually divided into the following families: the Procynosuchidae (I am including genera which have been placed in separate families by some authors, e.g. Silphedestidae, Dviniidae, Cynosauridae); the Galesauridae; the Cynognathidae; the Chiniquodontidae (this family probably includes most of the South American carnivorous cynodonts which have not yet been adequately described but which are at present being studied by Prof. A. S. Romer); the Trirachodontidae; the Diademodontidae; and the Traversodontidae. The interrelationships and time-spans of these families are shown in Figure 1. The last three families are commonly referred to as the gomphodont cynodonts and it is only in them that complex occlusion between upper and lower postcanine teeth occurred. Postcanine occlusion is present in the Ictidosauria, but it is not complex. The Traversodontidae were the most varied and abundant of the cynodonts and their remains have been discovered in the

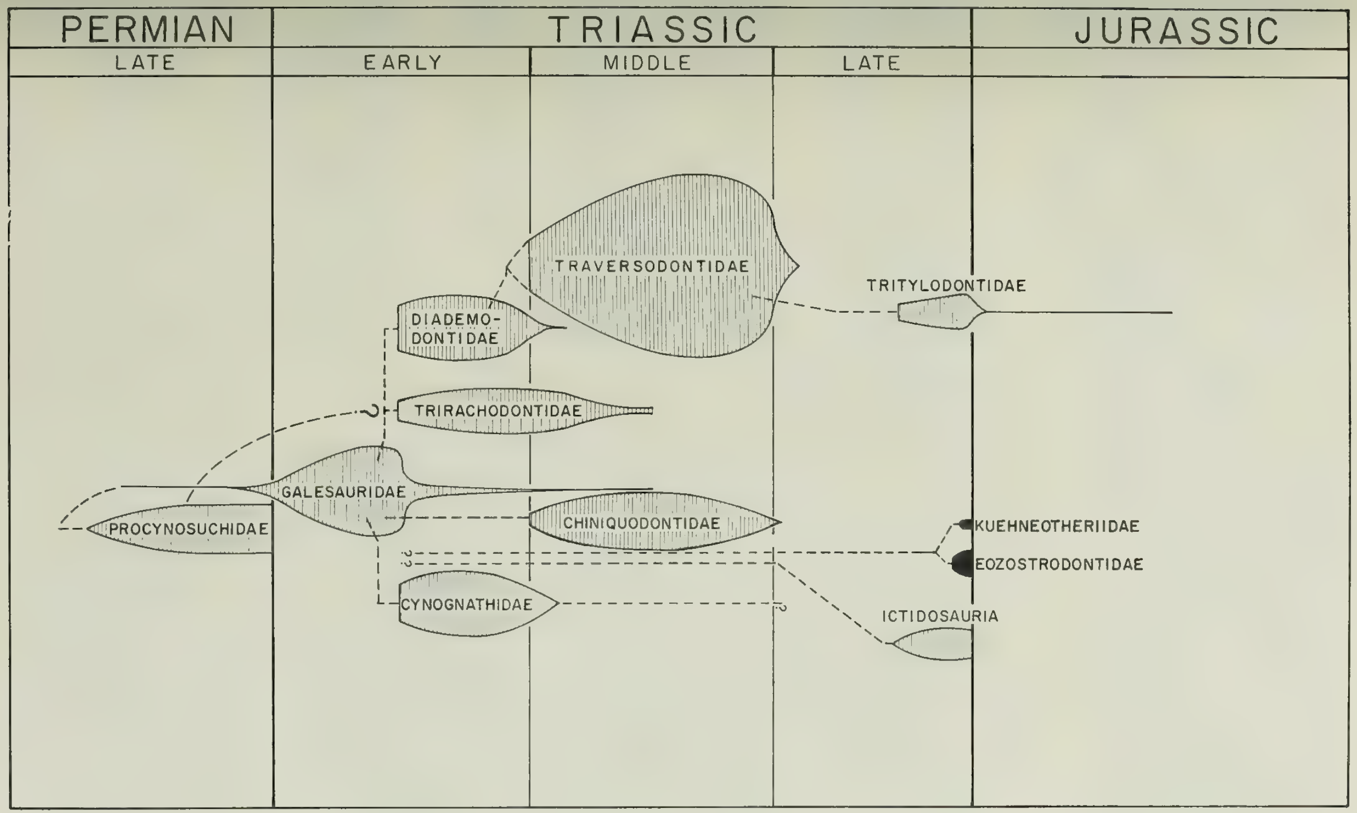

Fig. 1. Time-spans and interrelationships of the major cynodont families (vertically hatched). Also shown are the two earliest mammal families (black), the Kuehneotheriidae and the Eozostrodontidae; apparently these were related to early cynodonts but no intermediate forms are known.

Middle Trias of East Africa, Late Trias of South Africa and in great abundance in the Trias of South America (see Crompton, 1955; Crompton & Ellenberger, 1957; Bonaparte, 1967a & b; Romer, 1967; and Sill, 1969 for pertinent literature). Numerous representatives of the remaining cynodont families have been found in the sedimentary rocks of the Karoo system of South Africa (Haughton & Brink, 1954 and Lehman, 1961 for pertinent literature), although they are also known from South America (Bonaparte, 1967a & b), China (Young, 1959 & 1961) and Russia (Tatarinov, 1968). Dental occlusion (i.e. tooth-to-tooth contact) is absent in the Procynosuchidae and Galesauridae but, as members of these families are ancestral to the later gomphodont cynodonts, their postcanine dentitions will be briefly considered.

II. POSTCANINE DENTITION OF THE PROCYNOSUCHIDAE AND GALESAURIDAE

The postcanine dentition of the Procynosuchidae is best known in the South African species *Leavachia duvenhagei*. In a recent review of procynosuchid literature Anderson (1968) suggested that *Procynosuchus*, *Galecranium* and *Galeophrys* were probably synonymous with *Leavachia*; the postcanine row of *Leavachia duvenhagei* consisted of 7 to 11 teeth according to the age of the individual. Alternate tooth replacement was observed in all specimens studied.

Mendrez (1967) figured the postcanines of an unidentified species of *Leavachia*. The crowns of postcanines from the middle of the row were circular in cross-section while those further back were longitudinally ovate (Fig. 2A). A large external cusp was present. On the internal edge of the crowns of both upper and lower teeth there was a series of small cusps, the most anterior and posterior of which were visible in external view; in this view therefore, the crown appeared to be tricuspid. In lateral view it could be seen that upper and lower postcanines alternated with one another; the centre of the lower tooth lay medial to the space between two upper teeth. The lower postcanines bit medial to the uppers but because there was no contact between upper and lower teeth matching shearing surfaces did not develop. The postcanines of these early cynodonts were therefore capable of gripping, puncturing and possibly crushing food but could not shear food efficiently.

The postcanine dentition of the aberrant procynosuchid *Dvinia prima* from the Russian Permian was described in detail by Tatarinov (1968), who placed the genus in a new family Dviniidae. The postcanine teeth were considerably more complex than those of *Leavachia*. The crowns of the upper postcanines ("molars") (Fig. 2B). were transversely ovate with a central cusp completely surrounded by several small cusps on the edge of the crown. Unlike those of *Leavachia* these cusps were present on the external edge of the crown as well as on the internal edge and the external cusps were slightly larger than the internals. The lower molars of *Dvinia prima* were similar to the uppers except that additional cusps were present in the centre of the crown medial to the main cusp. The postcanines of *Dvinia prima* could have been derived from those of *Leavachia* by the addition of a series of small external cusps. In *Dvinia* upper and lower canines did not occlude, i.e. there was no tooth-to-tooth contact, and the lower postcanines bit medial to the uppers. In these respects the teeth of *Dvinia* were superficially similar to those of *Leavachia*. Because

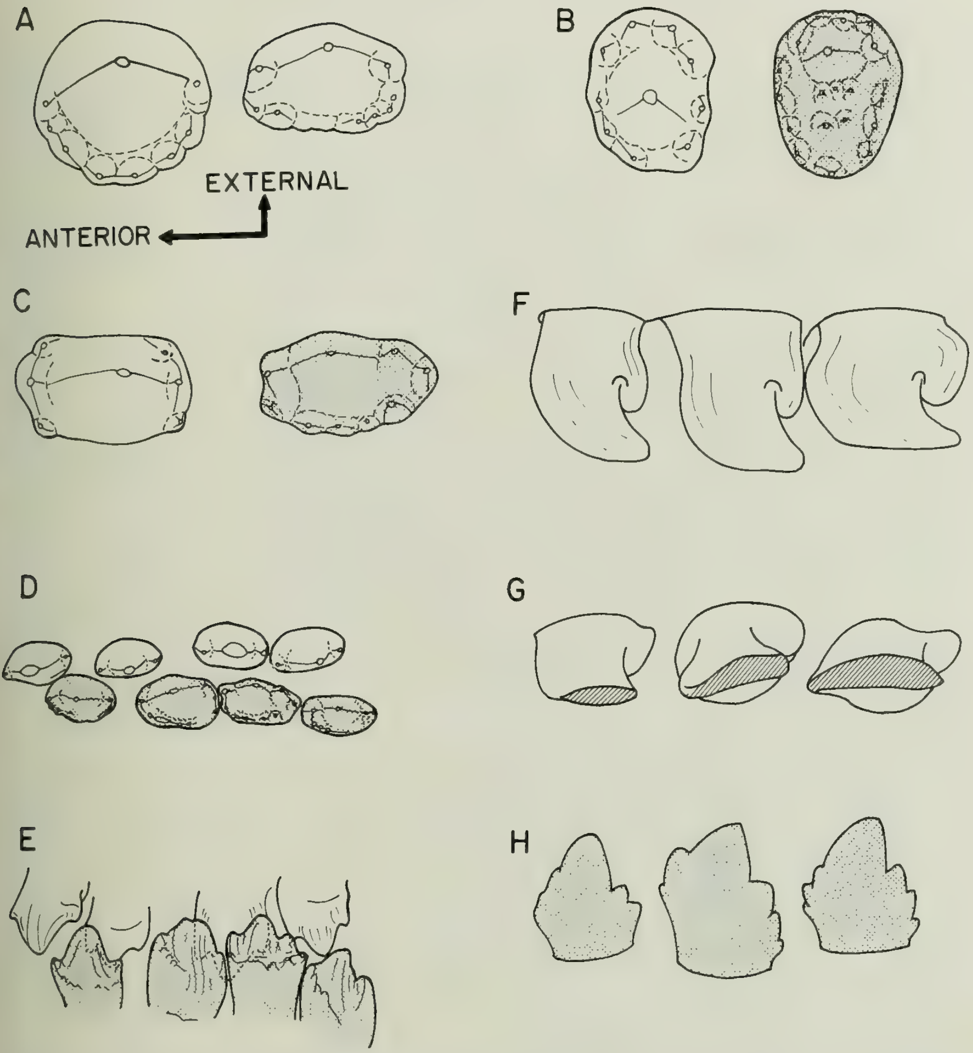

Fig. 2. Galesaurids and procynosuchids. Postcanine teeth. (In these and all other text-figures lower teeth are stippled, upper teeth are plain). A. *Leavachia.* Crown view of upper from middle and back of row. After Mendrez, 1967. B. *Dvinia prima.* Crown views of upper and lower. After Tatarinov, 1968. *C. Thrinaxodon.* Crown views of upper and lower. D. *Thrinaxodon.* Crown views of last four uppers and last four lowers. E. *Thrinaxodon.* Internal views of last four uppers and last four lowers. F. *Glochinodontoides gracilis.* External view of first three uppers. G. *Glochinodontoides gracilis.* Crown view of first three uppers. H. *Cynidiognathus.* External view of posterior lower postcanines. After Fourie, 1964.

the teeth were transversely ovate they appear to be similar to those of gomphodont cynodonts, but in the latter group crown-to-crown occlusion was present.

Several small Permian cynodont skulls have been described (e.g. *Protocynodon, Nanictosuchus, Nanictosaurus, Silphedestes*; see Haughton & Brink, 1954 for pertinent literature). These appear to have had postcanine teeth similar to those of the galesaurid *Thrinaxodon liorhinus* but until they have been adequately prepared and studied their taxonomic position will remain in doubt. It is possible that the forerunners of the Galesauridae will be found among these little-known cynodonts.

The best-known member of the Galesauridae is *Thrinaxodon liorhinus*. Several undistorted skulls of this species have been prepared with acetic acid and the crown patterns and relationships of upper and lower postcanines studied in detail. The postcanine teeth did not occlude, replacement was alternate, their crowns were longitudinally ovate and both upper and lower crowns (especially the lowers) had a well developed internal cingulum which supported several cusps. In Fig. 2C, D & E and Plate 1 the postcanines are shown in crown and internal view. It will be seen that the upper and lower teeth tended to alternate with one another in position and that when the jaws were closed a considerable space separated the outer surface of the lower teeth and the inner surface of the upper teeth. All the specimens studied showed this. As in procynosuchids, the postcanines of *Thrinaxodon* did not develop matching wear facets on the internal surface of the uppers or external surface of the lowers, thus indicating that shearing did not take place; i.e., upper and lower teeth did not occlude with one another. Lateral movement of the lower jaws sufficient to enable upper and lower teeth to come into contact appears to have been prevented in both Galesauridae and Procynosuchidae by the strong transverse processes of the pterygoids and the large pits in the palate which accommodated the lower canines. *Tribolodon* from the younger *Cynognathus* zone had postcanine teeth similar to those of *Thrinaxodon* but the internal cingulum of the lower postcanines was reduced and, in the material available for study, I never observed more than two subsidiary cusps on the internal surface of either upper or lower postcanines.

The postcanine teeth of the remaining galesaurid genera, i.e. *Galesaurus, Glochinodon, Glochinodontoides, Platycraniellus* and *Cynosuchoides*, were distinct from those of *Thrinaxodon*. Upper and lower teeth (Fig. 2F, G; Plate 2) were apparently identical and were characterized by a strongly recurved main cusp with a sharp blade-like cusp behind and by a total absence of subsidiary cusps on the anterior or internal surfaces. The tip of the main cusp was worn but, as in *Thrinaxodon*, there were no matching shearing surfaces on upper and lower teeth. In a few specimens available for study teeth were being replaced, but there appears to have been a "break-down" of the alternate tooth-replacement pattern that characterized *Thrinaxodon* and the procynosuchids. The way in which these peculiar teeth functioned is not understood.

Galesauridae with teeth of this type may have been ancestral to the Cynognathidae or Chiniquodontidae. In *Cynognathus* and *Cynidiognathus* (Fourie, 1964) the postcanines usually lacked internal cingula; the main cusp was slightly recurved (Fig. 2H); and, depending upon the position of a postcanine in the tooth row, one, two or three anterior and posterior accessory cusps may have been present. In *Cyno-*

gnathus there was no obvious alternate replacement of the postcanines but the presence of matching wear facets on the external surface of the lowers and internal surface of the uppers shows that the teeth were used for shearing.

III. POSTCANINE DENTITION OF THE DIADEMODONTIDAE AND TRIRACHODONTIDAE

The earliest known cynodont to develop postcanines with a complex occlusal pattern was the gomphodont cynodont *Diademodon* from the early Trias of South Africa. The dentition has been described by Seeley (1895), Watson (1911), Broili & Schröder (1935) Brink (1955, 1957), Crompton (1955, 1963), Fourie (1963, 1964), Hopson (1971) and Ziegler (1969). The postcanine row was differentiated into two to six conical teeth in front; three to nine transversely widened gomphodont teeth in the middle; and two to five posterior teeth which range in crown structure from semi-gomphodont to fully sectorial (Fig. 3B). The number of teeth present depended upon the age of the individual. The upper gomphodont teeth were transversely ovate in crown view and wider than the corresponding lower teeth (Fig. 3A–C and Plate 2B) so that, when the teeth occluded, the inner and outer margins of the upper teeth overlapped the corresponding margins of the lowers (Fig. 14C). The alternate tooth replacement characteristic of *Thrinaxodon* did not occur in *Diademodon*; the details of replacement in the latter genus are not yet fully understood, but it was complex, not alternate, and apparently confined to the anterior and posterior regions of the postcanine row. At the front of the row sharp conical teeth replaced worn gomphodont teeth; at the back gomphodont teeth replaced either semi-gomphodont or sectorial teeth. Consequently the occlusal relationships between upper and lower gomphodont teeth were never disturbed by replacement in the middle of the row as would have been the case if replacement had been of the alternate pattern found in the earlier Galesauridae.

Ziegler (1969) concluded that there was probably no replacement at the back of the postcanine row of *Diademodon*, the pattern being essentially mammalian in that only the incisors, canines and anterior postcanines were replaced. His paper was based entirely upon published accounts of the dentition. Ziegler correctly pointed out inconsistencies both in my own and in other authors' attempts to interpret the tooth replacement pattern that was present in *Diademodon*, but his conclusions too are open to criticism and do not appear to be substantiated by the known material.

Dr. J. Hopson of the University of Chicago is at present preparing a manuscript on tooth replacement in *Diademodon* and Dr. J. Osborn of the Dept. of Oral Anatomy, Guys Hospital, London, is completing a manuscript on the order of tooth eruption and replacement in *Diademodon* and some early cynodonts. Because of this I do not wish to enter here into a full discussion of tooth replacement in *Diademodon* but would like to point out some problems raised by Dr. Ziegler's interpretation.

In the smallest known specimen of *Diademodon* (Kitching, private communication) the postcanine row contains two or three gomphodont teeth and is terminated by two or three teeth which appear to have been either semi-gomphodont or sectorial in structure. In slightly larger specimens (Brink, 1963b) the postcanine row contains five gomphodont teeth with three semi-gomphodont or sectorial teeth behind. In still larger specimens (Crompton 1955, 1963b) up to seven gomphodont teeth are present with four or five semi-gomphodont or sectorial teeth behind. The *Diademodon* skulls of different sizes might be considered as different species but this is an extremely unlikely interpretation as many were found at one locality (Brink, 1963b); it is more reasonable to suppose that they represent growth stages of a single species (Kitching, 1968). Ziegler appears to have overlooked the size range of the available material of *Diademodon* and the fact that the postcanine row always ends in a series of teeth which become progressively more sectorial. It would be impossible to obtain the growth stages listed above without replacement at the back of the row. In the large series of jaws studied by Fourie (1964) there is clear evidence of the loss of some of the anterior conical postcanine teeth, and a specimen of *Diademodon* in East Berlin (Crompton, 1963b) clearly documents the replacement of the most anterior gomphodont tooth by a conical tooth. In 1955 I interpreted a longitudinally ovate opening below an unerupted posterior postcanine tooth of *Diademodon* as an alveolus, but it seems that Ziegler does not accept this as evidence of replacement of a sectorial tooth by gomphodont tooth at the back of the postcanine row.

Diademodon is closely related to other gomphodont cynodonts such as *Trirachodon*, *Cricodon*, *Scalenodon* and a new and as yet undescribed and unnamed reptile from the Ntawere Formation of the Luangwa Valley (Zambia). In a *Trirachodon* skull prepared by Dr. F. R. Parrington and figured by myself (1963a) there is clear evidence of the replacement of the sectorial teeth at the end of the postcanine row by gomphodont teeth. In a late survivor of the Trirachodontidae, *Cricodon* (Crompton, 1955), a longitudinally ovate foramen containing the root of a sectorial tooth lies below an unerupted gomphodont tooth; this foramen is similar in shape and position to that found in *Diademodon* but was clearly an alveolus and not a gubernacular canal. In some species of *Scalenodon* the postcanine row is terminated by small gomphodont teeth; unerupted larger gomphodont teeth lay above the small teeth and would presumably have replaced them later. This evidence, derived from growth stages of *Diademodon* and from related forms that have been figured or studied in South Africa, suggests that the posterior postcanine teeth were replaced during growth. *Diademodon* may eventually have reached a mature stage when replacement ceased in the postcanine series and this may explain why in several of the larger individuals there is no clear evidence of replacement at the back of the row. Ziegler is perhaps unaware that most of the available *Diademodon* material is poorly preserved and has undergone little or no development; careful preparation of the existing material will probably show teeth that were in the process of being replaced at the time of death.

The important points concerning *Diademodon* are that gomphodont teeth were lost in front (or were replaced by conical teeth); that they were added behind (by the replacement of existing semi-gomphodont or sectorial teeth); and that there is no evidence of replacement of gomphodont teeth by gomphodont teeth. Consequently, a series of gomphodont teeth always shows a progressive increase in wear towards the front; this is because of the occlusal relationships of the postcanine teeth. The replacement patterns of teeth in gomphodont cynodonts ensured that in *Diademodon* a fresh supply of cusped gomphodont teeth were added during growth and that in the later forms a fresh supply of teeth with deep shearing planes were added. In gomphodonts the enamel covering the crowns of the teeth appears to have been thin and perhaps soft, so that the structure of the crown was soon worn away and the teeth were perhaps replaced more rapidly than in mammals.

The exact order of tooth replacement occurring in the ontogeny of *Diademodon* is not fully understood; it is hoped that further work on material already available will clarify this process and meet the objections raised by Dr. Ziegler.

Crown views of unworn upper and lower gomphodont teeth of *Diademodon* are given in Fig. 3A and Plate 2. The upper crowns were transversely ovate whereas the lower crowns tended to be more circular. The upper crown was dominated by an external main cusp from which a well-defined ridge ran directly forwards, bearing two or three subsidiary cups which became smaller towards the front; another ridge, ill-defined and slightly crenulate, ran backwards from the tip of the external main

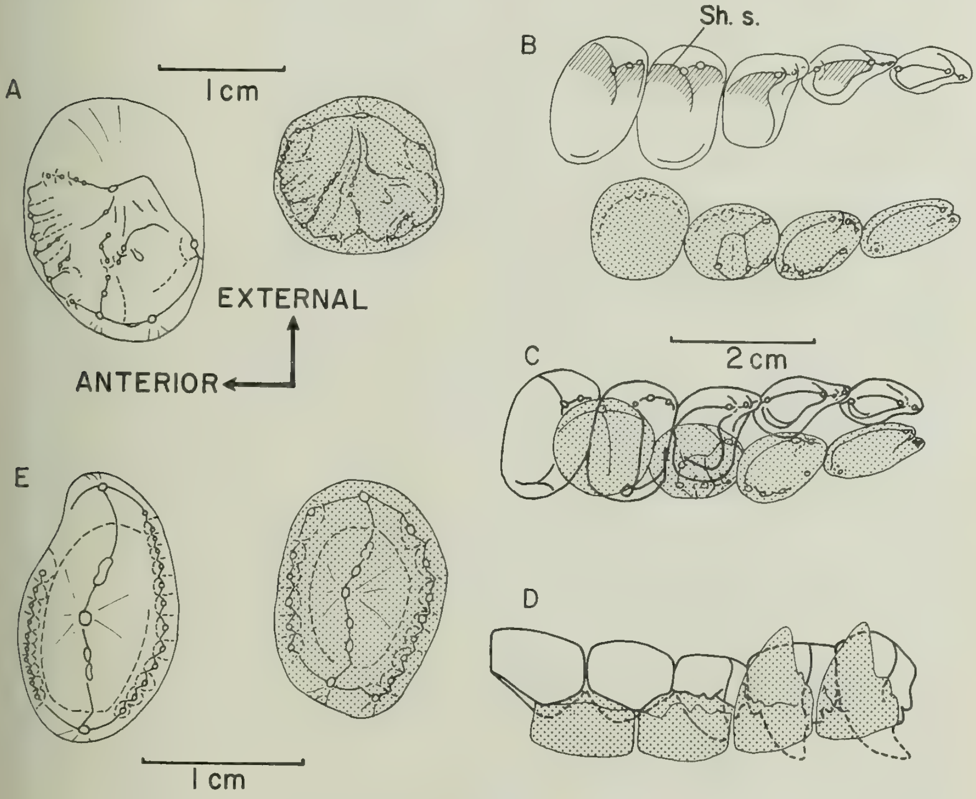

FIG. 3. Diademodontids and trirachodontids. Postcanine teeth. *A*. *Diademodon*. Crown view of typical upper and lower gomphodont teeth. B. *Diademodon*. Crown views of last five uppers and last four lowers to show shearing surfaces produced by wear. C. As in B, but superimposed as when occluded. D. As in C, occluded, but in internal view. E. *Cricodon*. Crown views of typical upper and lower. For key to abbreviations see p. 69.

cusp. The internal edge of the crown was dominated by two cusps, the anterior and posterior internal cusps, which, although smaller than the external cusp, were almost as high. The anterior edge of the crown bore a series of four or five small cusps which tended to become bigger towards the mid-line. The posterior edge supported one or two well-defined cusps of unequal size and a series of small cuspules or crenulations. A series of crenulated ridges radiated from the centre of the crown towards both the anterior and the internal cusps, with shallow valleys or basins lying between. A series of three or four smaller ridges radiated from the base of the external main cusp towards the centre of the crown to terminate in an ill-defined high area which supported a series of small cusps and which, together with the ridges radiating from the external and internal cusps, formed an ill-defined transverse ridge. A shallow occlusal basin was formed between the transverse ridges of two consecutive teeth, the ridge running backwards from the main cusp of the anterior tooth and the ridge running forwards from the main cusp of the posterior tooth.

The crowns of the lower gomphodont teeth of *Diademodon* were similar to those of the upper. Each had an external main cusp from which a ridge ran backwards, supporting one or two cusps which became smaller towards the back. A weak ridge ran forwards from the main cusp to terminate in a prominent cusp on the antero-external edge of the crown. A prominent cusp was present on the middle of the internal edge of the crown connected with the base of the main cusp by a ridge running transversely across the crown. Ridges supporting smaller cuspules radiated medially from the main cusp. A series of cusps was present on the anterior edge of the crown, from each of which a ridge ran backwards; they became bigger towards the mid-line. The central region of the crown was relatively high and flat.

The unworn crowns appear to have been capable of crushing and puncturing food and it seems that the details of the crown pattern were quickly worn away in most *Diademodon* specimens. The enamel of *Diademodon* postcanines was extremely thin. The external main cusp of the lowers pounded into the basin formed between two adjoining upper postcanines (Figs 3C & 14) and, as wear proceeded, insignificant vertical shearing planes (Sh.s.) were developed between the external surface of the lower cusp and the internal surfaces of the ridges running forwards and backwards from the external main cusps of two adjoining upper teeth (Figs 3B & 14). As the external main cusps were worn down, these planes were lost and the anterior gomphodont teeth were reduced to featureless nubbins of dentine. In several primitive mammals, e.g. *Eozostrodon* and *Tinodon* (Crompton & Jenkins, 1967, 1968), occlusal planes were established by destroying major features of the crown.

The gomphodont postcanine teeth of *Diademodon* were followed by a series of three or four teeth which became progressively more sectorial towards the back, that is, the inner extension of the crown became progressively smaller. During occlusion the main cusp of the first semi-gomphodont lower tooth met the crown of the matching semi-gomphodont upper tooth internal to the main cusp of the latter and slightly behind the gap between the last gomphodont tooth and first semi-gomphodont tooth. The occlusal details of the posterior postcanines are illustrated in crown view in Fig. 3C and in internal view in Fig. 3D. As the lower jaw closed, shearing was possible between the outer surface of the main cusp of the lower semi-gomphodont tooth and the inner surface of the main cusp of the upper. However, as the tip of the main cusp of the lower tooth abutted against the occlusal surface of the internal extension of the corresponding upper cusp, it was rapidly worn down and its shearing function reduced. In the more advanced traversodonts the lower jaw was pulled backwards as the teeth came into occlusion; this postero-dorsally directed power stroke may have been initiated in *Diademodon*.

The postcanine dentition of *Diademodon* showed a significant advance beyond the galesaurid condition.[1] The lower teeth lay directly below the crowns of the upper rather than internal to them. The cusps of upper and lower postcanines could therefore be used more effectively for puncturing and crushing food. In addition, matching vertical shearing surfaces were present on both the gomphodont series and the sectorial series of postcanine teeth; these were rapidly obliterated by wear but this was compensated for by the type of tooth replacement present in *Diademodon* which ensured that new gomphodont and sectorial teeth either replaced existing teeth at the back of the row or were added thereto. The gomphodont postcanines of *Diademodon* may be derived from those of early galesaurids or procynosuchids by widening the teeth in a lingual direction. The Lower Triassic cynodonts *Pascualgnathus* and *Andescynodon* recently discovered in South America by Bonaparte (1967b) may throw considerable light on the evolution of the *Diademodon* type of postcanine tooth from those of earlier cynodonts.

The postcanine teeth of *Trirachodon* of the South African Lower Trias and of *Cricodon* of the East African Middle Trias were slightly different from those of *Diademodon*. The postcanine row consisted of six or seven transversely ovate gomphodont teeth with two or three sectorial teeth behind. There was a sharp break between these two series; the transitional zone present in *Diademodon*, where the teeth become progressively more sectorial towards the back, was absent. The upper and lower gomphodont teeth in *Trirachodon* (Fig. 14) and *Cricodon* (Fig. 3E and Plate 3) had three main cusps, an external, a central and an internal arranged to form a prominent transverse ridge across the crown. The anterior and posterior margins of the crown each bore a row of small cusps. The faint ridges which ran forwards and backwards from the external and internal main cusps of the uppers were not worn by the lowers to produce the vertical shearing surface seen in *Diademodon*; some degree of shearing may have been present between the sectorial teeth, but these were so small in comparison with the gomphodont teeth that it could not have been significant. The gomphodont teeth were presumably used to puncture and crush. The transverse ridges of the upper and lower teeth alternated with one another during occlusion but the wear facets suggest that they could not have sheared effectively.

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[1] I have assumed that *Diademodon* was derived from a galesaurid similar to *Thrinaxodon*. This assumption is based upon the similarity of the sectorial teeth of *Diademodon* to the teeth of *Thrinaxadon* and upon the anteroposterior alignment of the cusps on the external edge of the upper teeth of *Diademodon*. It is based also on the fact that galesaurids were the dominant cynodonts of the *Lystrosaurus* zone and that as a family they represent a distinct advance over the procynosuchids of the earlier *Kistecephalus* zone. However, some or all of the gomphodont cynodonts may have arisen directly from the Procynosuchidae (Bonaparte, 1963); this would explain the single external cusp on the gomphodont teeth of the Trirachodontidae.

In the Trirachodontidae there was no alternate tooth replacement and, as in *Diademodon*, new gomphodont teeth were added behind to replace sectorial teeth.

IV. POSTCANINE DENTITION OF THE TRAVERSODONTIDAE

Until recently relatively little was known about Middle to Late Triassic therapsids (Crompton 1955, 1963B); recent work in South America, South Africa and East Africa, however, has led to the discovery of numerous therapsid remains, most of which have still to be described. It is now clear that the gomphodont cynodonts of the family Traversodontidae were the dominant cynodonts during the Middle Trias and early part of the Late Trias. The basic pattern of the crowns of the postcanine teeth of the traversodontids is characteristic of the group and separates it very clearly from the earlier gomphodont cynodonts. Relatively minor differences in the dentition and occlusal relations distinguish the genera of traversodontid cynodonts from each other, the structure of the postcanines providing a useful key for identifying genera and species and for determining the relationships and evolutionary history of the group. Like those of diademodontids, the postcanines of traversodontids were subjected to severe wear which in most cases eventually obliterated all details of the crown pattern. It will be shown below that the wear of the crowns of traversodontid postcanines resulted from a combination of complex occlusal relationships and jaw movements. The occlusion of traversodontid postcanines closely paralleled that of primitive mammals with tribosphenic molars. The abundance and diversity of traversodontids during Middle Triassic times may have been partly due to their highly evolved masticatory apparatus.

In an earlier paper (Crompton 1955) three new genera of cynodonts (*Scalenodon*, *Cricodon* and *Aleodon*) and several indeterminate remains were described from the Manda Formation of Tanzania. No attempt was made to classify them above the generic level. Romer (1967) has recently revised the classification of gomphodont cynodonts; it is now apparent that *Scalenodon angustifrons* and the isolated maxilla with two teeth which I compared with the South American genus *Gomphodontosuchus* should both be included in the family Traversodontidae, while *Aleodon brachyrhamphus* is clearly not a traversodontid and *Cricodon metabolus* appears to have been a surviving member of the Trirachodontidae. This accords with a view expressed by Bonaparte (1963). Subsequently Brink (1963a) described a gomphodont, *Luangwa drysdalli*, from the Ntawere Formation of Zambia; it is not well preserved and the occlusal aspects of the teeth are not known, but it appears to have been closely related to *Scalenodon angustifrons*, if not actually identical. In 1963 the British Museum (Natural History)—University of London Joint Palaeontological Expedition (Attridge, Ball, Charig & Cox, 1964) collected additional material from the Ntawere Formation of Zambia and the Manda Formation of Tanzania; at least one new genus and two new species of traversodontid cynodonts were discovered as well as additional specimens of *Scalenodon angustifrons* and *Aleodon brachyrhamphus*. I hope to give a full description of this new material in a later publication. Meanwhile, because the postcanine teeth of all the East African traversodontids (including the new material) are discussed below, the new specimens have been named and briefly described in order to avoid future confusion.

1. Description of three new species of *Scalenodon* from the Middle Trias of East Africa

Family **TRAVERSODONTIDAE** von Huene 1936

Genus ***SCALENODON*** Crompton 1955

Type-species. *Trirachodon angustifrons* Parrington 1946.

Since I first described *Scalenodon* (Crompton 1955 : 647) other genera have been discovered in East Africa, South Africa and South America which are closely related to it. Because of this the original diagnosis given for *Scalenodon* is no longer applicable, several of the supposedly diagnostic features mentioned having subsequently proved to be diagnostic of the family Traversodontidae as a whole rather than of the genus *Scalenodon* in particular. A revised diagnosis for *Scalenodon* is therefore given below.

This diagnosis is based entirely upon the characters of the upper postcanine teeth; it does not include features of the lower postcanine dentition because the latter is not known in all species of the genus. A detailed description of the rest of the skulls and skeletons of the several species of *Scalenodon* is now projected; this may necessitate some revision of the classification suggested in this paper.

Diagnosis. Small to medium-sized traversodontid cynodonts in which the upper postcanine teeth are transversely ovate; the external margin of the crown is gently convex; two main cusps are present (external and internal), the latter lying at the internal end of a prominent transverse ridge which usually supports an additional (central) cusp; small antero-external and antero-internal cusps are occasionally present; the inner surfaces of the external cusps form a vertical, antero-posteriorly aligned shearing surface, towards which the accessory cusp does not contribute substantially (contrast South American traversodontids); anterior and posterior cingula are present; during the power stroke of occlusion the backward movement of the lower jaw was limited so that matching transverse ridges, upper and lower, were never drawn across one another.

Comments. The upper postcanines of the four species of *Scalenodon* show some striking similarities to those of various genera of traversodontid cynodonts from South America. The type-material from both continents is at present being studied in order to determine, if possible, whether those similarities are due merely to convergence or to a closer phylogenetic relationship than is indicated by the present classification.

S. angustifrons (Parrington). Material of this species includes not only the holotype (Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 120B) but also a number of other specimens which I referred to it when proposing the genus (Crompton 1955). Details of horizon and localities are given and discussed in the same work. Now that three new species of *Scalenodon* have been recognized (see below) it is possible to give a specific diagnosis for *S. angustifrons*. The diagnostic characters of all four species are compared in Table 1. Note also that in *S. angustifrons* there is a ridge of small cuspules on the outer surface of the main cusp of the upper postcanines.

TABLE 1

	S. angustifrons	*S. hirschsoni*	*S. attridgei*	*S. charigi*
Text-figure:	4C	7A	10A	10C
position of tooth-row:	curving away from mid-line posteriorly	nearly parallel to mid-line	curving away from mid-line posteriorly	unknown
setting of teeth in maxilla:	not oblique	not oblique	oblique	very oblique
shape of gomphodont teeth in crown view:	inner region never wider than outer	more rectangular than in *S. angustifrons*	inner region wider than outer	anterior and posterior margins roughly parallel
transverse ridge:	behind middle of tooth, high with steep anterior and posterior walls, supports external and central cusps	more posterior in position than in *S. angustifrons*, lower, supports external and central cusps	still more posterior in position, supports external and central cusps	forms part of posterior edge of crown, central cusp appears to be absent
external and internal anterior accessory cusps:	absent	present	external small, internal large	both large, connected by high anterior wall
anterior cingulum:	poorly developed	well developed	well developed forms cuspidate anterior wall in posterior postcanines	well developed, forms non-cuspidate anterior wall
posterior cingulum:	poorly developed	well developed	well developed but less prominent than in *S. hirschsoni*	poorly developed

Scalenodon hirschsoni sp. nov.

Plate 5; Text-figs 7–9

Derivation of name. In honour of Dr B. Hirschson, who was a member of the British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, 1963, and who has done so much to help vertebrate palaeontologists and archaeologists working in southern Africa.

Material. Only the holotype in the British Museum (Natural History), Pal. Dept. regd. no. R. 8577. Field catalogue no. U12/3/26. Partial skull with well-preserved postcanine teeth.

Horizon. Manda Formation (Middle Trias, probably Anisian).

Locality. Ruhuhu Valley, S.W. Tanzania: Locality U12 of the B.M.(N.H.)—University of London Joint Expedition, 1963. Between the Hiasi and Njalila streams, just south of the Rutukira River; the most northerly of the Expedition's localities west of the Njalila.

Description. See Table 1 for diagnostic characters. Note also that the incisors and canines, both upper and lower, are procumbent. The postcanines are described in greater detail on p. 49.

Scalenodon attridgei sp. nov.

Plate 6; Text-figs 10A, B

Derivation of name. In honour of Mr John Attridge, of Birkbeck College, London, who was a member of the British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, 1963, and who made many of the discoveries of that expedition, including the unique specimen of this species.

Material. Only the holotype in the British Museum (Natural History), Pal. Dept. regd. no. R. 8578. Field catalogue no. U2/2. A beautifully preserved snout with complete upper dentition; probably a young individual.

Horizon. Manda Formation (Middle Trias, probably Anisian).

Locality. Ruhuhu Valley, S.W. Tanzania; Locality U2 of the B.M.(N.H.)—University of London Joint Expedition, 1963. Immediately next to the Peramiho–Litumba dirt road, on its left (south-western) side; low in the K8, before the Expedition's turn-off to Njalila and Mkongoleko, and probably only about a mile before the K7 boundary.

Description. See Table 1 for diagnostic characters. Note also that the anterior edge of the unworn crown of the upper postcanines bears a row of five distinct cusps, of which the innermost is the largest. The postcanines are described in greater detail on p. 53.

Scalenodon charigi sp. nov.

Text-fig. 10C

Derivation of name. In honour of Dr Alan J. Charig, Curator of Fossil Reptiles in the British Museum (Natural History), who initiated and participated in the B.M.(N.H.)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika in 1963.

Material. Only the holotype in the Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 136. Part of a left maxilla in which two postcanine teeth are preserved.

Horizon. Manda Formation (Middle Trias, probably Anisian).

Locality. Ruhuhu Valley, S.W. Tanzania; Locality B26 of Stockley (1932 : 620). Gingama, south of the Ruhuhu River.

Description. See Table 1 for diagnostic characters. Note also that the central main cusp of the upper postcanines *appears* to be absent (this part of the tooth is damaged).

Comments. This specimen was described and figured by Crompton (1955 : 659–660, fig. 14E), who compared it with the Brazilian species *Gomphodontosuchus brasiliensis*. It is now clear that its postcanine teeth are distinct from those of the other Ruhuhu traversodontids; the antero-external and internal accessory cusps are better developed than in the other East African forms, the antero-external forming part of a vertical shearing surface. It is therefore desirable, despite the smallness of the preserved portion, to base a new species on this specimen.

S. charigi is similar in some respects to *Gomphodontosuchus brasiliensis* but is nevertheless distinct from that too. The postcanine teeth, though smaller, closely resemble those of the South American genera *Exaeretodon* and *Gomphodontosuchus*; the matching transverse ridges, however, did not cross one another during the power stroke of occlusion as they did in *Exaeretodon* and *Massetognathus*.

2. Occlusion and jaw movements in the primitive traversodontid *Scalendon angustifrons*

The most primitive traversodontid postcanines known are those of *Scalenodon angustifrons*.[2] Although the dentition of this species has been described in detail (Crompton 1955), the new material discovered by the 1963 Joint Expedition has revealed many features of the postcanines and their occlusion which were not dealt with before.

Fig. 4 shows three views of typical upper and lower postcanines of *S. angustifrons*; stereo-photographs are given in Plate 4.

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[2] If *Andescynodon* and *Pascualgnathus* described by Bonaparte (1966, 1967*b*) are considered as traversodontids, then these should be regarded as the most primitive members of the family. I, however, should prefer to place them in the Diademodontidae.

Upper teeth. These consisted essentially of three cusps arranged to form a transverse row, the central cusp being nearer the inner side of the crown. The internal (i.c.u.) and central (c.c.u.) cusps formed a high, prominent transverse ridge (t.r.) with anterior and posterior surfaces nearly vertical; a deep embayment (e.) separated this ridge from the external cusp (e.c.u.). A sharp ridge (a.r.) running forwards from the apex of the external cusp had a nearly vertical inner face which formed the outer border of a deep valley (a.v.) in the anterior surface of the tooth,

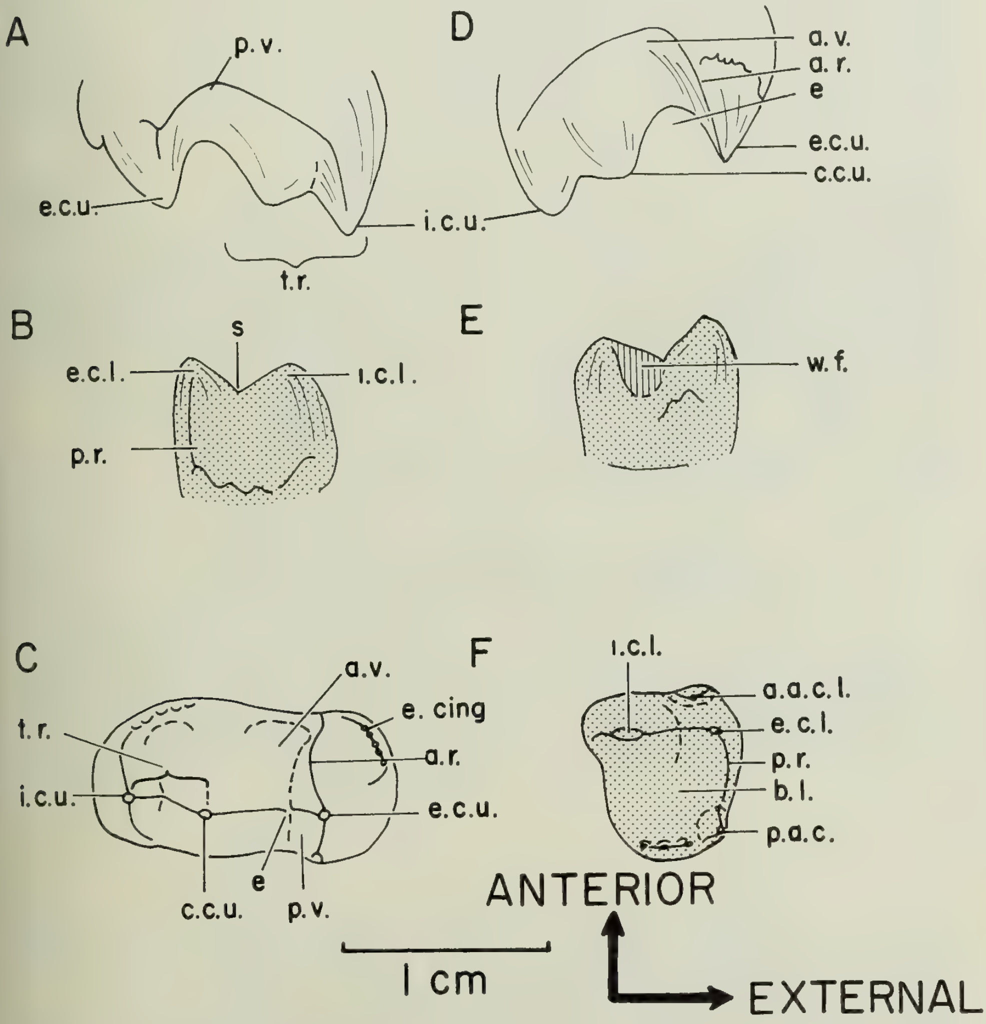
A
p.v.
e.c.u.
i.c.u.
t.r.
D
a.v.
a.r.
e
e.c.u.
c.c.u.
B
s
e.c.l.
i.c.l.
p.r.
E
w.f.
C
a.v.
t.r.
e. cing
a.r.
i.c.u.
e.c.u.
e
c.c.u.
p.v.
F
i.c.l.
a.a.c.l.
e.c.l.
p.r.
b.l.
p.a.c.
ANTERIOR
1 cm
EXTERNAL

FIG. 4. *Scalenodon angustifrons*. Postcanine teeth. A. Posterior view of upper. B. Posterior view of lower. C. Crown view of upper. D. Anterior view of upper. E. Anterior view of lower. F. Crown view of lower. For key to abbreviations see p.69

immediately in front of the embayment between the external and central cusp (see Fig. 4D). A smaller, less well defined valley (p.v.) occupied a corresponding position behind the transverse ridge. The anterior valley of one postcanine and the posterior valley of the preceding tooth together formed a deep occlusal basin with high anteroposteriorly aligned shearing surfaces.

Lower teeth. The crown of a lower postcanine of *S. angustifrons* consisted of two high anterior cusps, the external (e.c.l.) being higher than the internal (i.c.l.); a high ridge ran backwards along the outer surface of the crown (p.r.) from the apex of the external cusp, its outer surface being more or less vertical. The external and internal cusps were connected by a transverse ridge which dipped down to a saddle between them; the anterior surface of this ridge was nearly vertical. A deep basin (b.l.) lay behind the two main cusps, rimmed posteriorly by a row of small cuspules of which the outermost (p.a.c.) was the largest. A small anterior accessory cusp (a.a.c.l.) was present on the anterior surface of the crown.

Occlusion. In Fig. 6 several opposing postcanines are shown in crown view and oblique internal view at the beginning of dynamic occlusion (A, B, respectively) and at the end (C, D). At the beginning of dynamic occlusion the anterior surface of the transverse ridge formed by the two main cusps of the lower tooth sheared past the posterior surface of the transverse ridge formed by the central and internal main cusps of the preceding upper tooth. (In Fig. 6B lower postcanine 6 is shearing

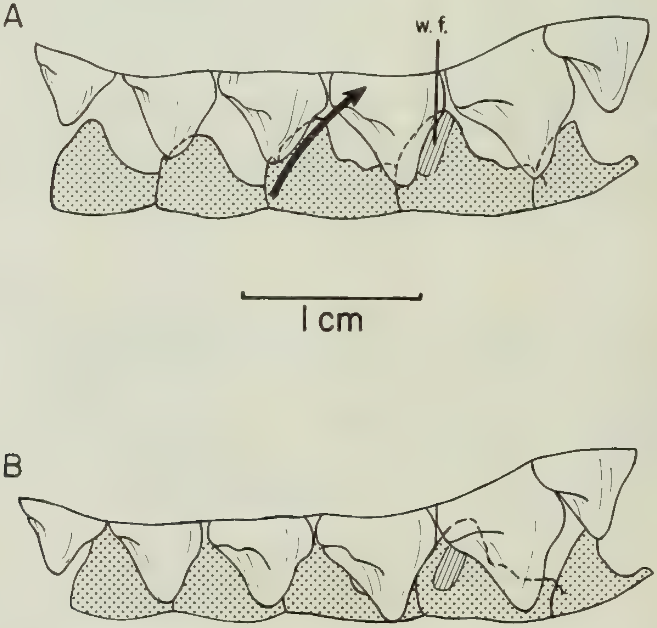

Fig. 5. *Scalenodon angustifrons*. Lateral views of postcanine teeth, showing the posterodorsal direction of the power stroke. A. At the beginning of dynamic occlusion. B. At the end of dynamic occlusion.

against upper postcanine 5). This produced wear facets on the front of the transverse ridge of the lowers and on the back of the transverse ridge of the uppers. The central cusp of the upper tooth fitted into a groove on the anterior surface of the lower tooth between the two main cusps. The outer surface of the external main cusp of the lower tooth sheared past the posterior portion of the vertical internal surface of the external main cusp of the preceding upper postcanine; the position of the postcanines at the beginning of dynamic occlusion as seen in lateral view is given in Fig. 5A, which shows the resulting striations (w.f.) on the outer surface of the external main cusp of the lowers. As the jaws continued to close (Figs 5B and 6D) the lower jaw moved slightly backwards as well as upwards so that the external surface of the lowers sheared past the anterior portion of the vertical internal surface of the external cusp of the corresponding upper postcanine tooth. The arrows in

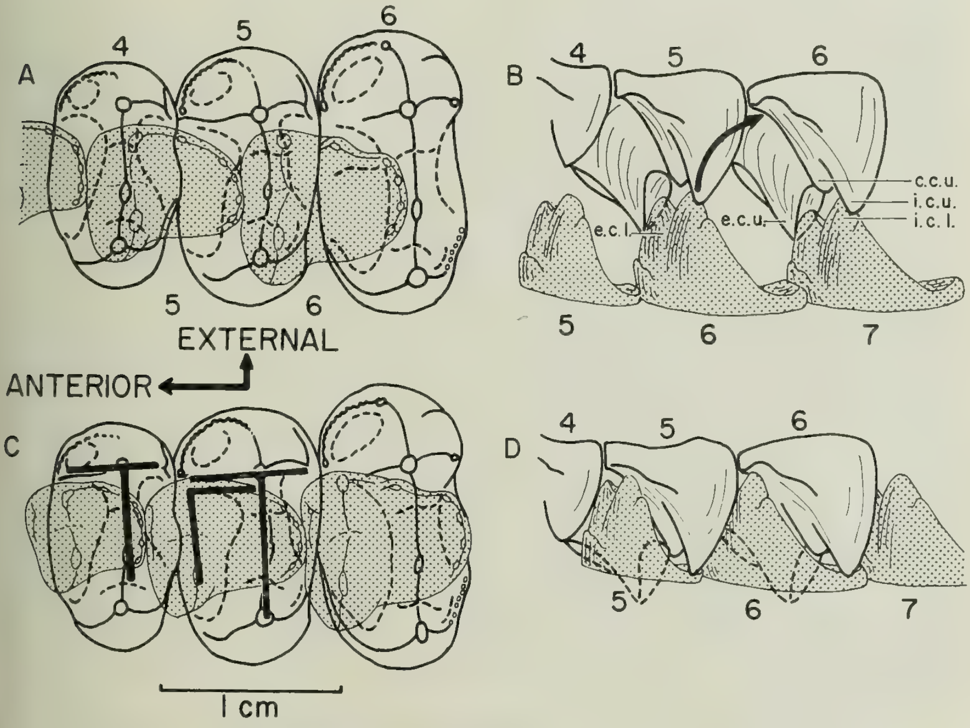

FIG. 6. *Scalenodon angustifrons*. Details of tooth occlusion. The numbers 4 to 7 indicate the positions of the teeth in the postcanine series. A. Crown views of the postcanines at the beginning of dynamic occlusion, with upper and lowers superimposed. B. Oblique internal view of the same. The heavy arrow indicates the passage of the tip of the internal main cusp of the lower teeth during dynamic occlusion. C. Crown views of the postcanines at the end of dynamic occlusion, with uppers and lowers superimposed. The main transverse and longitudinal shearing surfaces are drawn in heavy lines. D. Oblique internal view of the same. For key to abbreviations see p. 69.

Figs 6B and 5A indicate the direction of movement of a single lower postcanine during the final stages ("power stroke") of occlusion. The posterior surface of the external cusp of the lower tooth and the anterior surface of the external cusp of the corresponding upper formed two opposing crescents when seen in lateral view (Fig. 5A). Such an arrangement is ideal for cutting provided that the lower jaws moved slightly backwards during occlusion. An analogous arrangement typified the shearing surfaces of tribosphenic molars (Crompton & Hiiemäe, 1969b). When the postcanines of *S. angustifrons* were in tight occlusion (Fig. 6, C and D) the external main cusp of a lower postcanine lay in the valley (Fig. 4D, a.v.) in the anterior surface of the corresponding upper postcanine and the central cusp of the upper lay above the posterior basin of the lower. The dentition of *S. angustifrons* was characterized also by the addition of new gomphodont teeth with shearing surfaces behind and by the loss of worn postcanines in front. The replacement pattern was similar to but simpler than that of *Diademodon*.

The occlusal pattern of *S. angustifrons* represented a distinct advance over that of *Diademodon*. Not only were transversely orientated shearing planes added, but the occlusal basin of the upper postcanines was considerably deepened by the development of deep valleys immediately internal to the external main cusp. Consequently the tip of the main cusp of the lower postcanine was not worn down as rapidly as it was in *Diademodon*, where it abutted directly against the crown surface of the occluding tooth. Deepening the occlusal basin also increased the height of the shearing surfaces.

The postcanines of *S. angustifrons* therefore consisted essentially of a series of transversely and longitudinally orientated shearing planes. The positions of these shearing planes on upper and lower postcanines are indicated by heavy lines on Fig. 6C. Occlusion in other traversodontid cynodonts and tritylodontids was basically a modification of the arrangement that was present in *Scalenodon angustifrons*. The tips of the cusps were used for puncturing, the sides of several of the cusps for shearing and the posterior heel of the lower posterior postcanines provided a firm basin for crushing, analogous to the talonid basin of the tribosphenic molar. The potscanines of *S. angustifrons* were therefore functionally similar to the tribosphenic molars of primitive mammals. In mammals with tribosphenic molars and in some of the insectivores and herbivores with more specialized molars the jaw moves not only vertically during occlusion but also transversely and forwards in order to utilize a series of shearing plates. In *S. angustifrons* the mandible moved vertically and slightly *posteriorly* during occlusion and thereby also utilized a series of shearing planes.

It is generally assumed that in primitive cynodonts the tympanic membrane was partially attached to the posterior surface of the quadrate (see Hopson, 1966 for a complete review of this problem). The posterior movement of the jaw during dynamic occlusion in *S. angustifrons* was apparently too great to be accommodated within the available space between the glenoid of the articular and the condyle of the quadrate. Parrington (1946) suggested that in *Thrinaxodon* and later cynodonts the quadrate itself must have been capable of antero-posterior movement but recognized that such movement would have torn or stretched the small tympanic membrane because the stapes rested against the quadrate. In a new skull of *S. angustifrons* (B.M.(N.H.) R. 8579), discovered in 1963 in Tanzania, it can be seen that the quadrate was held in a groove in the squamosal and could slide both downwards and forwards; the amount of movement of which it was capable appears to have been sufficient to have allowed the mandible to be pulled backwards a little during the final stages of dental occlusion. Kemp (1969), following on the earlier work of Parrington (1955), has shown that the quadrate was extremely mobile in gorgonopsians too so that, despite the firm junction between the articular and the quadrate, the mandible was capable of antero-posterior movements during mastication; a mobile quadrate was presumably present in all cynodonts and therocephalians. In *S. angustifrons* the external auditory meatus presumably lay in a groove of the squamosal and, as Parrington (1946) has shown, the groove was terminated by a semicircular lip which supported the tympanic membrane without involving the posterior surface of the quadrate. Movement of the quadrate would therefore not have involved the tympanic membrane directly, but this does not solve the problem completely as the stapes was presumably in contact with both tympanic membrane and quadrate, and stapes and quadrate may have moved together. Unfortunately the relationship between the stapes and the quadrate of advanced cynodonts is not well known, but the removal of the tympanic membrane contact from the quadrate to the squamosal in primitive traversodontids may be related to the antero-posterior movements of the mandible which appear to have taken place during occlusion.

The postcanine tooth rows of *S. angustifrons* diverged backwards. Consequently antero-posteriorly aligned cutting surfaces of opposing teeth would have tended to separate during extensive backward movement of the lower jaw and for this reason the amount of antero-posterior movement during occlusion in *S. angustifrons* was probably small. It is doubtful whether the jaw could have swung far enough laterally to retain contact on one side. A mobile mandibular symphysis would have overcome this limitation, but the nature of the fossil material suggests that the two rami were firmly united. The fossilized remains of *S. angustifrons* consist of numerous fragments, indicating that the skeletons of this animal were usually scattered and broken before fossilization; despite this the mandibular rami are usually found fused at the symphysis, as would not be expected had the symphysis been mobile during life. By contrast, the mandibular rami of tritylodontids and early mammals are seldom if ever preserved fused at the symphysis, which suggests that the latter was mobile. Szalay (1969) has argued that primitive primates too had a mobile symphysis because Palaeocene primate mandibles are usually preserved separated.

3. Occlusion and jaw movements in *Scalenodon hirschsoni*

The only known specimen of *S. hirschsoni* is ideal for the study of occlusion because it yielded to preparation with acetic acid; the lower jaw was thereby freed from the remainder of the skull. It was possible to study details of the structure of the teeth, the wear facets and occlusal relationships. Among the features of this species which clearly separate it from *S. angustifrons* are that the upper incisors and lower canines are slightly procumbent and that the postcanine rows are nearly parallel to one another, the last postcanine lying immediately in front of the transverse process of the pterygoid. The basic structure of the crowns of the postcanines (Figs 7A, B, 8; Plate 5) is essentially the same as that of *S. angustifrons*. The crowns of the upper postcanines are relatively longer antero-posteriorly than those of *S. angustifrons* and the portion of the crown lying in front of the transverse ridge is considerably wider

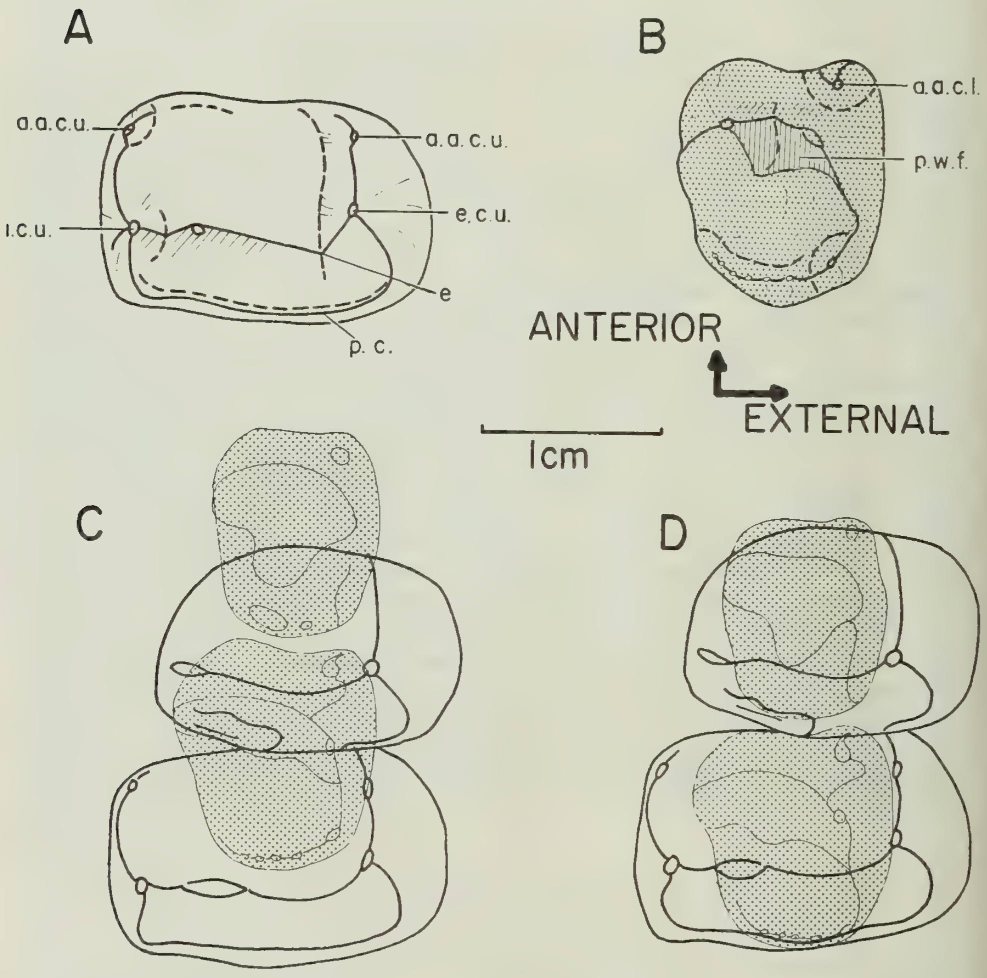

Fig. 7. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A. Crown view of upper. B. Crown view of lower. C. Crown views of uppers and lowers superimposed to show the relative positions at the beginning of dynamic occlusion. D. The same, at the end of dynamic occlusion.

than the portion behind; this is probably due more to addition to the anterior part of the crown than to a posterior migration of the transverse ridge because small additional cusps (a.a.c.u.) are present on the ridges running forwards from both external and internal main cusps. The embayment between the external and central main cusps (Fig. 8A) is deeper than that of *S. angustifrons* and the transverse ridge is not as high as in the latter species. A fairly prominent posterior cingulum (Fig. 7A, p.c.) is present.

In the lower postcanines (Fig. 7B) the transverse ridge formed by the two main cusps is not as high as that of *S. angustifrons* and the anterior accessory cusp (a.a.c.l.) is larger. Details of occlusion and of the amount of longitudinal movement during mastication are illustrated in Figs 7C–D, 8A–D and 9A–E. Because the transverse ridge of the uppers also is lower than in *S. angustifrons* and because it was apparently worn down fairly rapidly, its posterior surface does not form a high wall (see internal views of beginning and end of dynamic occlusion, Fig. 8C–D); nevertheless small matching wear facets on that surface and on the anterior surface of the transverse ridge of the lower postcanines indicate that some shearing took place in this position. The mandibular movements which probably took place during occlusion have been reconstructed by manipulating the opposing jaws and by studying the striations on the wear facets of opposing teeth. These movements are illustrated in Fig. 9 in external view by showing several positions of the lower postcanines 5 and 6 relative to the upper postcanines 4 and 5. As the jaws closed, the anterior part of the external surface of the main cusps of lowers 5 and 6 sheared past the internal surfaces of the external main cusps of uppers 4 and 5 (Fig. 9A–B). As the mandible proceeded backwards (Fig. 9B–C–D) the external surface of the external main cusp of lower postcanine 5 sheared past the internal surface of the external main cusp of upper postcanine 5. This shear, as it would have appeared in internal view, is illustrated in Fig. 8C–D. The wear facets on the external surface of the lower postcanines resulting from this backward movement are shown in Fig. 9F. The important point is that at the beginning of dynamic occlusion the transverse ridge of the 5th lower postcanine lay behind the transverse ridge of the 4th upper postcanine (Fig. 7C). In essence, therefore, occlusion resulted from a posterior and a vertical jaw movement, just as in *S. angustifrons*. However, a lightly worn 5th lower postcanine of *S. hirschsoni* shows a distinct wear facet (Fig. 7B, p.w.f.) on the *posterior* surface of the main cusp; this matches a wear facet on the *anterior* surface of the transverse ridge of the 5th postcanine. It is difficult to account for these facets if the power stroke of the lower jaw was directed dorso-posteriorly. Admittedly they could have resulted from the postero-dorsal surface of the transverse ridge of the lower tooth being drawn backwards and downwards across the antero-ventral surface of the transverse ridge of the upper. This movement, as it would appear in external view, is shown in Fig. 9D. Although this would have involved crushing between the opposing transverse ridges, it would have required that the lower postcanines be dragged down an inclined plane. The same wear facets, however, would have been formed if the mandible had moved forwards and upwards during dynamic occlusion as shown in Fig. 9E so that the leading edge of the transverse ridge of the lowers sheared past the trailing edge of the transverse ridge of the uppers. This movement

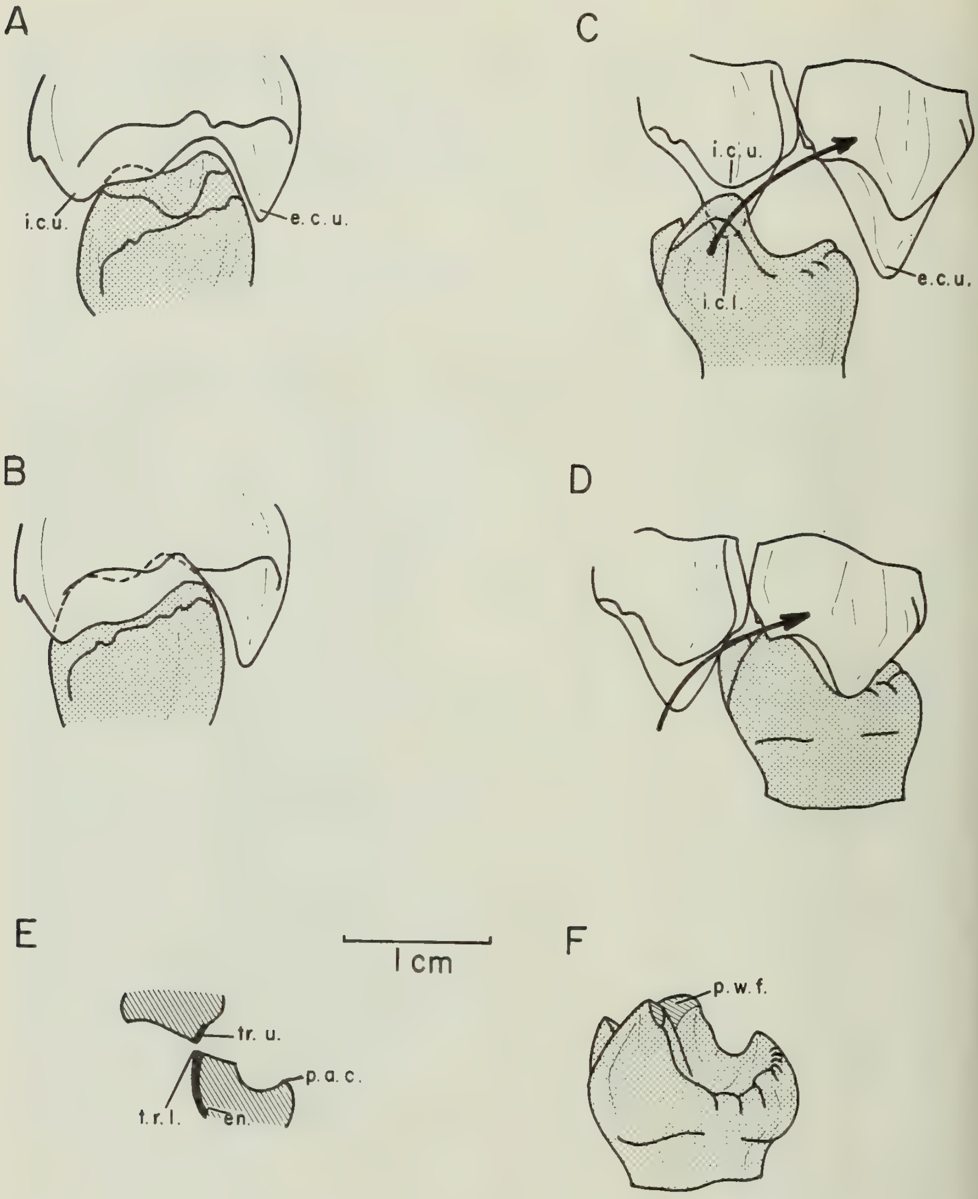

FIG. 8. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A. Posterior view at the beginning of dynamic occlusion. B. Posterior view at the end of dynamic occlusion. C. Oblique internal view at the beginning of dynamic occlusion. D. Oblique internal view at the end of dynamic occlusion. E. Sagittal section through part of opposing postcanines to show matching shearing surfaces resulting from anteriorly directed power stroke. F. Internal view of lower postcanine to show wear facet resulting from anteriorly directed power stroke.

as it would appear if a longitudinal section were cut through the teeth, is shown in Fig. 8E; the enamel-like material (en.) is considerably thicker on the anterior surface of the transverse ridge of the lower tooth than on the occlusal surface or in the posterior basin, just as would be expected if this species were capable of a forwardly directed power stroke as well as the usual backwardly directed stroke.

4. Postcanine dentition of *Scalenodon attridgei*

This species is known only from an isolated snout, with the upper teeth well preserved on both sides. The postcanine row (Fig. 10A, B, Plate 6) of eight teeth ends behind in three teeth which become progressively smaller, as in many specimens of *S. angustifrons*. The first five teeth are so worn that most of the details of crown structure are lost, but the 6th and 7th postcanines are only slightly worn and the 8th not at all. Although the last two teeth are smaller than the more anterior ones and would presumably have been replaced later in life by larger gomphodont teeth, they are of great interest. The basic pattern of the postcanines of *S. attridgei* is similar to that of *S. angustifrons* and *S. hirschsoni*. They are, however, set obliquely in the maxilla, and the internal surface is slightly wider than the external surface. The

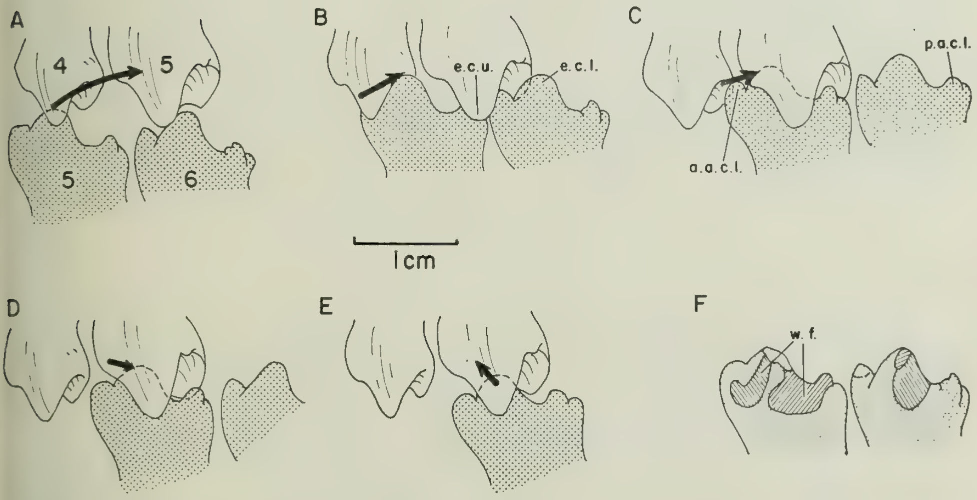

FIG. 9. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A–D. External views to show successive stages of the posteriorly directed power stroke. Heavy arrow in A indicates total extent of backward movement involved. E. D. The same, but to show anteriorly directed power stroke. F. External view of lower teeth to show wear facets on the external surfaces.

important feature of the upper postcanines of S. *attridgei* is the presence of a row of well developed cuspules along the anterior border of the crown of postcanines 7 and 8; in postcanines 5 and 6 they have been obliterated by wear. The antero-medial cuspule (a.a.c.u.) is the largest of these cuspules and they tend to become smaller towards the exterior (Fig. 10B). A high ridge joins the external main cusps to the most external cuspule of the anterior row. The central and internal main cusps (c.c.u. and i.c.u.) are both large and well differentiated and form the transverse ridge. A basin (b.u.) is present in the occlusal surface of the crown; this is bordered behind by the transverse ridge, in front by the anterior row of cuspules and externally by the vertical inner wall of the external main cusp. A deep valley separates the internal main cusp and the most internal cuspule of the anterior row (a.a.c.u.) so that the basin is completely surrounded except for this narrow valley opening internally. In the 7th postcanine the tips of the central and internal main cusps and the tips of the cuspule forming the anterior ridge are worn away. In the more anterior teeth wear has tended to obliterate the original details of the crown pattern and especially the anterior row of cuspules. The tips of the central and internal main cusps and the crest of the transverse ridge have been worn away so that the occlusal surface of the crown in front of the transverse ridge is a plane sloping slightly upwards in an antero-external direction; this is best seen in the anterior view of the upper postcanines (Fig. 10B). Except for two internal cuspules, most of the cuspules of the anterior row of the 6th postcanine have been worn away and only a low wall remains. A feature of the crown of the 5th and 6th postcanines which is not present in the smaller 7th and 8th is a faint posterior ridge or cingulum (p.c.) close to the posterior margin of the crown. A shallow valley which widens slightly towards the external side lies anterior to it; this will be referred to as the posterior basin (p.b.). The wide forward and upward sloping flat surfaces of the crowns of the upper postcanines of S. *attridgei* could have resulted from both antero-dorsal and postero-dorsal power strokes. The postcanines of the Brazilian species *Traversodon stahleckeri* (von Huene 1944 : 48) are extremely worn, but from what remains of the upper teeth they appear to have been similar to those of S. *attridgei*.

5. Postcanine dentition of *Scalenodon charigi*

This specimen, consisting of an isolated maxilla with two posterior postcanines, was previously compared (Crompton, 1955) with the Brazilian species *Gomphodontosuchus brasiliensis*. Although the teeth were badly damaged several details can still be seen, and, now that more traversodontids from South America and East Africa have been described and figured, additional comments may be made.

The teeth (Fig. 10C) are set obliquely in the maxilla. The external anterior accessory cuspule (a.a.c.u.) is larger than in S. *hirschsoni* and the internal surfaces of the two external cusps form a high shearing surface. The main transverse ridge is situated near the posterior edge of the crown. The central cusp appears to be absent. The anterior wall is high and is terminated internally by a high rounded cuspule (a.a.c.u.); consequently the anterior basin (b.u.) is deep and occupies most of the occlusal surface of the crown. The shearing surface on the internal face of the external cusp is continuous with that on the posterior surface of the anterior wall of the same tooth; this suggests that the anterior surface of the transverse ridge of the corresponding lower postcanine sheared up the anterior wall of the upper postcanine rather than across it. Although the anterior wall was present in *S. attridgei*, it was

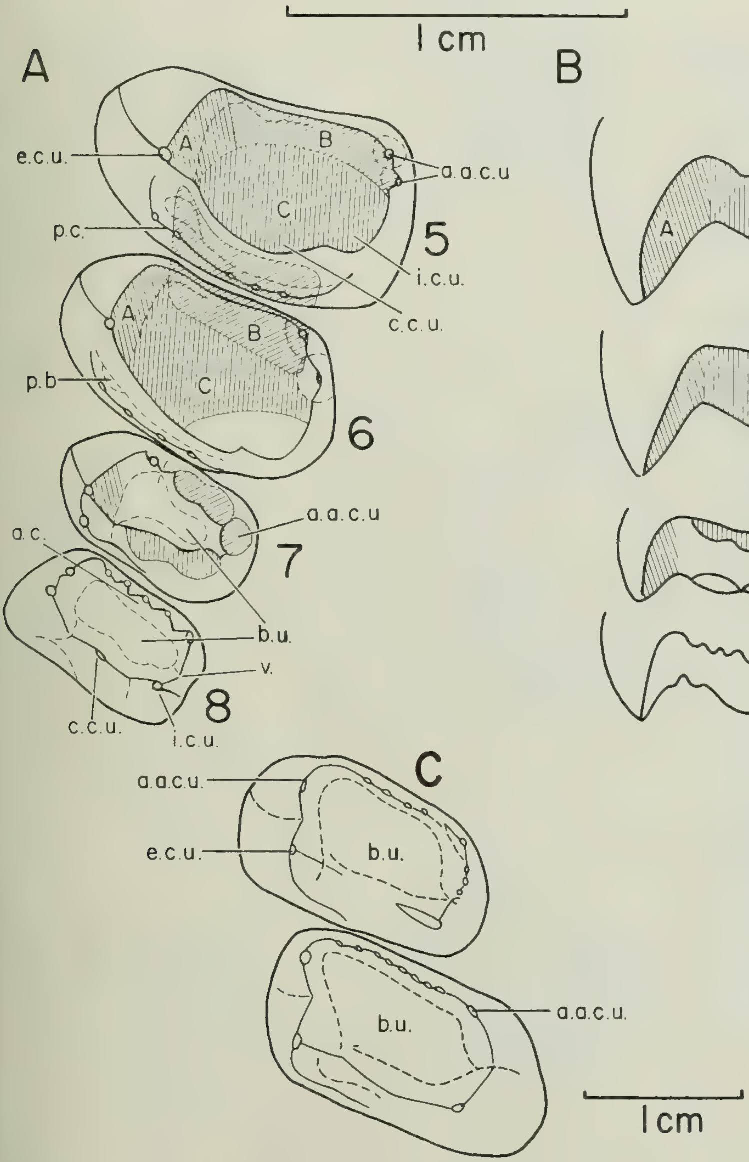
1 cm
A
B
e.c.u.
A
B
a.a.c.u
C
p.c.
5
i.c.u.
c.c.u.
A
B
C
p.b
6
a.a.c.u
7
a.c.
b.u.
v.
8
c.c.u.
i.c.u.
A
C
C
a.a.c.u.
e.c.u.
b.u.
b.u.
a.a.c.u.
1cm

FIG. 10. A. *Scalenodon attridgei* sp. nov. Crown view of last four upper postcanines. B. *Scalenodon attridgei* sp. nov. Anterior views of the same. C. *Scalenodon charigi* sp. nov. Crown view of last two upper postcanines. For key to abbreviations see p. 69.

rapidly worn away and apparently did not form a significant vertical shearing surface. The structure of the anterior wall, the absence of a central cusp and the oblique position of the crown relative to the longitudinal axis of the palate are reminiscent of the South American genus *Exaeretodon.*

6. Occlusion and jaw movements in a species of *Massetognathus*

The postcanines of the Argentine traversodontid *Massetognathus pascuali* have been described in detail by Romer (1967), but he does not discuss occlusion in detail. Dr. Bonaparte presented the Peabody Museum with a jaw fragment that has been tentatively assigned to the genus *Massetognathus,* and in which upper and lower postcanines were preserved in tight occlusion; the jaws have been carefully separated by Mr C. Schaff. Distinct wear facets are preserved on most of the teeth, and by matching upper and lower wear facets it has been possible to determine the jaw movements that must have taken place in *Massetognathus* during the final stages of the masticatory cycle. Although the postcanines are almost identical to those of *M. pascuali* the wear pattern is slightly different and the fragment should perhaps be placed in a different species or genus. This may be possible when the entire fauna of gomphodont cynodonts from Chañares is fully described.

The postcanines (Fig. 11 & Plate 7) are very similar to those of *S. angustifrons* except that two accessory cuspules rather than one are present on the ridge leading forwards from the external main cusp, which latter lies further back than in *S. angustifrons.* A characteristic feature of *Massetognathus* and *Exaeretodon* not present in the African traversodontids is that the external margin of the upper postcanines as seen in crown view is drawn outwards and backwards (Fig. 11B) to form a distinct lobe. The transverse ridge is high and forms the posterior border of the crown, the posterior cingulum being but poorly developed. The inner surface of the external main cusp and of the two anterior accessory cuspules forms a high vertical wall which is more pronounced than in *S. angustifrons.* The point of junction between the transverse ridge and the external main cusp lies near the posterior border of the crown. The lower postcanines are similar in structure to those of *S. hirschsoni* but lack the anterior accessory cuspules. As in all gomphodont cynodonts the amount of wear increases progressively towards the front of the jaw. Matching shearing planes are shown in Fig. 11D & E. As the teeth came into occlusion the outer surface of the 4th lower postcanine (Fig. 11D) sheared past the internal surface of the external main cusp of the 3rd upper postcanine (wear facets 2 in Fig. 11C, D & E); then, as the jaws continued to close, it also sheared past the inner surface of the two anterior accessory cuspules of the 4th upper postcanine (wear facets 1). The two facets, 2 and 1, on the 3rd and 4th upper postcanines respectively, are therefore continuous. This action was similar to that in *Scalenodon.* At the beginning of occlusion the tips of the two main cusps of the 4th lower postcanine lay anterior to the tips of the central and external main cusps of the 3rd upper postcanine, i.e. the transverse ridge of the lower lay in front of the transverse ridge of the upper (Fig. 14). The central cusp of the upper lay directly behind the valley separating the two lower cusps. Because of this, as the mandible was drawn back-

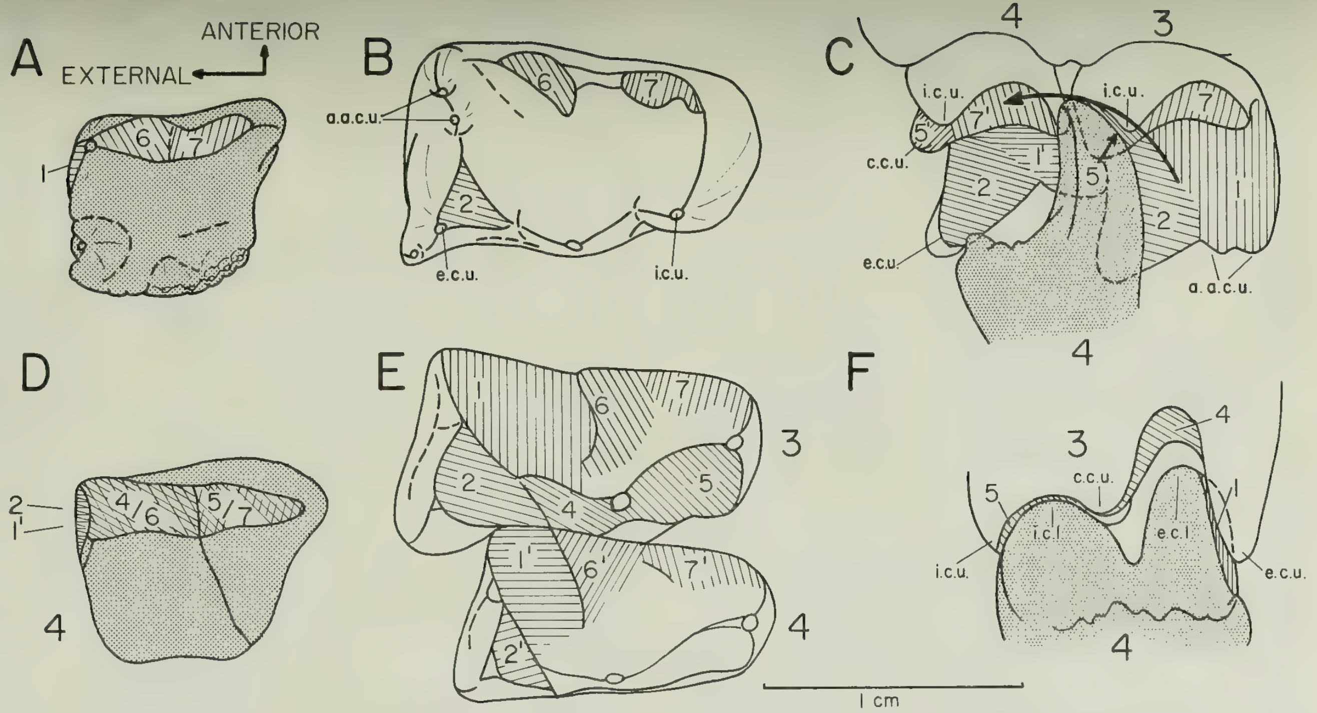
A
EXTERNAL
ANTERIOR
6
7
1
B
a.a.c.u.
6
7
2
e.c.u.
i.c.u.
C
4
3
i.c.u.
i.c.u.
5'
7'
7
c.c.u.
1'
2
5
2
1
e.c.u.
a.a.c.u.
4
D
2
1'
4/6
5/7
4
E
1
6
7
3
2
4
5
1'
6'
7'
2'
4
1 cm
F
3
4
c.c.u.
5
1
i.c.l
e.c.l
i.c.u.
e.c.u.
4

FIG. 11. *Massetognathus* sp. (specimen in Yale Peabody Museum). Postcanine teeth. A. Crown view of slightly worn lower. B. Crown view of slightly worn upper. C. Internal view to show the depth of the shearing surfaces on the internal faces of the external cusps of the upper teeth and the movement (heavy arrow) of a lower tooth relative to the uppers during the final stages of the power stroke.

D. Crown view of lower. } to show matching
E. Crown view of two uppers } shearing surfaces.
F. Posterior view of opposing pair at the beginning of dynamic occlusion.

wards and the lower cusps were dragged across the transverse ridge, pronounced wear facets were formed on either side of the central cusp of the uppers and on the tips of the main cusps of the lowers. These matching facets have been numbered 4 and 5 in both uppers and lowers (Fig. 11, D & E). As the mandible was drawn further back the main cusps of each lower tooth carved grooves into the anterior wall of the succeeding upper tooth. These grooves have been numbered 6^1 and 7^1 on the upper tooth (Fig. 11E) and the matching shearing surfaces 6 and 7 on the lower tooth (Fig. 11D). It is clear from the orientation of these matching facets that they were produced by the backward and upward movement of the mandible during the final stages of the masticatory cycle. A study of the wear facets in this species of *Massetognathus* therefore suggests that, as in *S. angustifrons*, the jaws were drawn backwards during dynamic occlusion; but those facets which suggest an anteriorly directed power stroke in *S. hirschsoni* and *S. attridgei* are absent in *Massetognathus*. Perhaps the most important feature of occlusion in this species of *Massetognathus* is that the transverse ridge of the lowers was drawn across the transverse ridge of the uppers. This was not the case in *Massetognathus pascuali*, *S. angustifrons* or *S. hirschsoni*, where the anterior surface of the transverse ridge of the lowers sheared up the posterior surface of the transverse ridge of the uppers. It is possible to derive the situation in the new species of *Massetognathus* from that in *S. angustifrons* simply by increasing the extent of the antero-posterior movement during occlusion. This is important when considering the ancestry of the tritylodontids.

7. Postcanines of *Exaeretodon* and *Gomphodontosuchus*

Bonaparte (1962) has described the teeth of *Exaeretodon frenguelli*; I was able to study postcanine teeth of this species in the Museum of Comparative Zoology at Harvard and at the Instituto Miguel Lillo in Tucumán. The upper postcanines (Fig. 12A, B, C) are similar to those of *Massetognathus*; and the postero-external extension of the external region is so marked that the tooth as seen in crown view may be divided into two lobes, a lateral and a medial. Well developed external (e.c.u.), anterior accessory (a.a.c.u.) and posterior accessory (p.a.c.) cusps are present on the external margin of the tooth; their internal surfaces form a continuous antero-posteriorly aligned shearing surface which extends right along the tooth from front to back. The transverse ridge terminates short of the base of the external main cusp; its central cusp is absent. Two anterior accessory cusps (a.a.c.u.) are present, one internal and one external. In posterior view (Fig. 12C) it can be seen that the crest of the transverse ridge rises very sharply ventrally towards the tip of the internal main cusp. The anterior wall (a.w.) of *Exaeretodon* is a prominent feature; it can be seen in anterior view (Fig. 12B) that it too rises very sharply ventrally to terminate in the internal anterior accessory cusp. A shallow basin separates this anterior wall from the transverse ridge. The cutting surface on the inner face of the external main cusp of each tooth is continuous with those in front and behind.

Because the anterior wall and the transverse ridge of each upper postcanine lie obliquely the internal main cusp of each lower postcanine is considerably further back than the external (Fig. 12D). Mandibular movements during dynamic occlusion were probably similar to those of *Massetognathus pascuali* and *Scalenodon angustifrons.* Wear facets indicate that the transverse ridges of the upper and lower postcanines were not drawn across one another from front to back but it appears that, instead, the primitive transverse shear still took place between the anterior surface of the transverse ridge of the lower tooth and the posterior surface of the transverse ridge of the upper. There is no indication that there was a forwardly directed power stroke. However it will not be possible to discuss jaw movements in *Exaeretodon* with any degree of confidence until the wear facets on the abundant postcanines have been studied.

The lower postcanines of the southern African traversodontid *Scalenodontoides macrodontes* Crompton & Ellenberger 1957 are almost identical in size and structure with those of *Exaeretodon. Scalenodontoides* was found in association with melanorosaurid (prosauropod) dinosaurs and is therefore younger than the East African traversodontids.

I have been unable to study the type of *Gomphodontosuchus brasiliensis* (von Huene 1944–48) and the following remarks are based upon stereophotographs of the specimen taken by Dr J. Hopson. This genus has exaggerated some of the features of the postcanines of *Exaeretodon.* The teeth are set in the jaw more

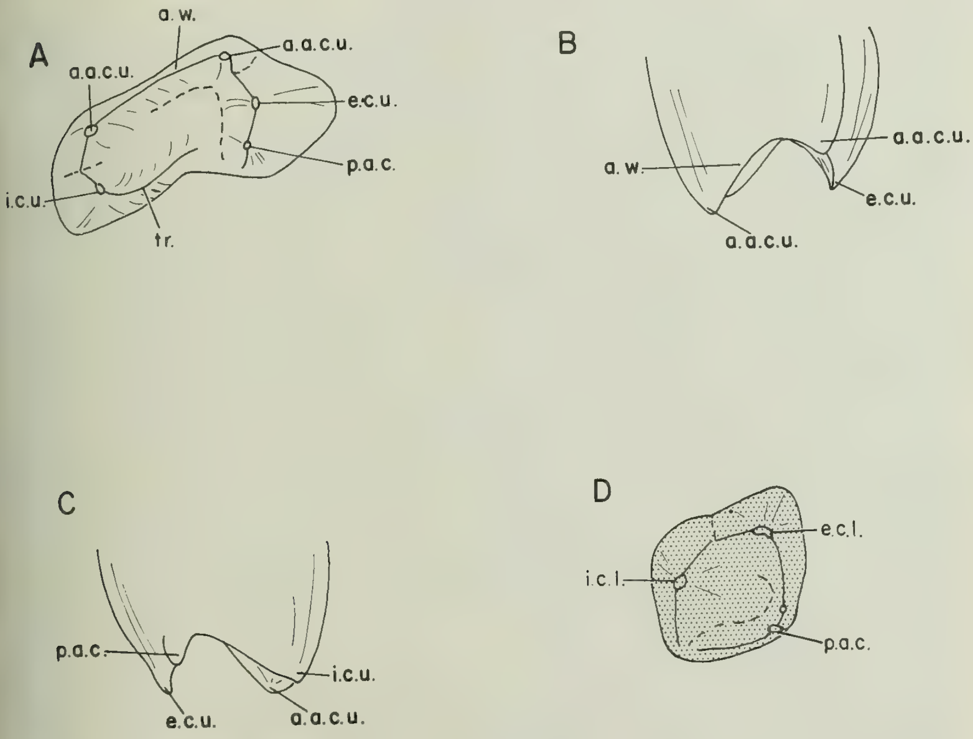

FIG. 12. *Exaeretodon frenguelli.* Typical postcanine teeth. A. Crown view of upper. B. Anterior view of upper. C. Posterior view of upper. D. Crown view of lower. For key to abbreviations see p. 69.

obliquely so that the angle between the transverse ridge and the inner shearing surface of the external cusp is smaller than in *Exaeretodon*; the obliquity is reflected also in the outline of the crowns of the lower postcanines. In *Gomphodontosuchus* the anterior wall of the upper postcanine is higher than in *Exaeretodon*, the crown basin therefore deeper; this presumably indicates an increase in the cutting function of the anterior wall.

V. DISTRIBUTION OF THE TRAVERSODONTIDAE

Traversodontids are known to have existed for a long period of time and their dentitions indicate that they occupied several different ecological niches. At present they are known with certainty only from Africa and South America; indeed, this is true of all gomphodont cynodonts, and it has therefore been suggested that they were restricted to the southern continents. However, a large lower jaw of what may prove to be traversodontid cynodont was discovered in the Upper Triassic Wolfville Formation of the Newark Group in Nova Scotia by Dr R. L. Carroll and Dr D. Baird (Romer, 1967); unfortunately no postcanine teeth were preserved *in situ*, but the size of the jaw and the structure of the symphysis showed close similarity to *Scalenodontoides macrodontes* from southern Africa.

The postcanine teeth of traversodontids from several horizons and numerous localities in Africa are remarkably similar to those of traversodontids from various localities in South America. *Scalenodon angustifrons* closely resembles *Massetognathus pascuali*; *S. charigi* closely resembles *Exaeretodon frenguelli* and *Gomphodontosuchus brasiliensis*; and *S. attridgei* closely resembles *Traversodon stahleckeri*. The traversodontids of the Chañares Formation (*Massetognathus*) are comparable in size to the various species of the East African *Scalenodon*, but, while no East African form approaches the gigantic size of the traversodontids from Ischigualasto (*Exaeretodon, Proexaeretodon* and *Ischignathus*), *Scalenodontoides* from southern Africa indicates that large gomphodont cynodonts were present on that continent during Late Triassic times. Unfortunately the traversodontids collected in Brazil (Colbert, 1963) have not yet been described. No African site has been discovered which has yielded traversodontids in anything like the abundance of those of South America.

The similarity of the terrestrial Early Triassic faunas from Argentina recently described by Bonaparte (1967*b*) and of terrestrial Middle Triassic faunas from various parts of South America to African faunas of corresponding age, including the cynodonts, may indicate a close connection—or at least easy migration routes—between Africa and South America during Triassic times. Recent views (Bullard 1969, Menard 1969) on the relative positions of the continental masses of Africa and South America before the end of the Cretaceous suggest that they were extremely close, if not united, during the Trias.

Early cynodonts (Late Permian to Early Triassic) are known from South America (Bonaparte, 1967*a*), South Africa (Haughton & Brink, 1954), East Africa (Parrington, 1936), China (Young, 1961), and Russia (Tatarinov, 1968). A carnivorous cynodont of Early to Middle Triassic age probably occurs in China (Young, 1959). The descendants of the cynodonts, the tritylodontids, have been discovered in Late Triassic deposits in South America (Sill, 1969), Africa (Fourie, 1968), China (Young, 1947), North America (Colbert, *pers. comm.*) and Europe (Kermack, 1965 and Kühne, 1956). Early mammals, also the descendants of cynodonts, have been discovered in the Late Triassic of southern Africa (Crompton, 1964), China (Rigney, 1963) and Europe (Kermack, 1965). In view of the world-wide distribution of these related groups it would not be expected that cynodonts should be totally absent from northern continents during Middle Triassic times. In particular, the gomphodont cynodonts may therefore have enjoyed a world-wide distribution; it may just be that their northern representatives (other than the jaw found by Carroll and Baird in Nova Scotia) have not been discovered as yet, and their apparent absence from northern continents may be due to the lack of suitable continental deposits of Middle Triassic age rather than to the absence of the animals themselves (Colbert, 1963).

The distribution of other Middle Triassic groups tends to support this view. For example, several Middle Triassic archosaurs are known from southern continents (Charig, 1967), but only a few, almost accidental finds are all that is known of the archosaurs of this age from northern continents (Krebs, 1965).

VI. OCCLUSION IN *TRITYLODON* AND THE ORIGIN OF THE TRITYLODONTIDAE

Several features of the skull and dentition of the traversodontids suggest that a member of this family may have been ancestral to the tritylodontids. This suggestion, made originally by Crompton & Ellenberger in 1957, is supported by the new material. The crowns of the upper cheek teeth of *Tritylodon* (Fig. 13J) consist essentially of three longitudinal rows of crescent-shaped cusps, three cusps each in the internal and central rows and two cusps in the external row. The corresponding lowers (Fig. 13K) consist of two rows each of three crescent-shaped cusps. The crescent of the upper cusps are concave forwards, whereas the crescents of the lower cusps are concave backwards (Fig. 13L). The two rows of lower cusps occluded between the three rows of upper cusps. Wear facets bearing parallel striations are developed on both surfaces of all the cusps except the outer surface of the external cusps of the uppers and the inner surface of the internal cusps of the uppers, which do not face any other surface; they indicate that during mastication the jaws moved horizontally. The extent of movement during occlusion is shown in Figs 13L and 14. The lower postcanine commenced dynamic occlusion by making contact with the upper tooth one position further forward in the upper jaw. The anterior edges of the upper cusps and the posterior edges of the lower cusps formed a multiple cutting mechanism which would have been effective only if the power stroke during mastication were directed backwards. Occlusion therefore involved the dragging of the tips of the central row of cusps of the upper teeth and of the tips of both rows of cusps of the lowers across the floors of the valleys between the longitudinal rows of cusps of the opposing teeth. As a result these crescentic cusps were rapidly worn down, thereby decreasing the shearing action of their near-vertical surfaces. In many specimens of tritylodontids the crowns of the postcanine teeth consist of almost flat surfaces scarred by longitudinal grooves. The backward jaw movements during occlusion, the rapid wearing down of teeth, the eruption of new teeth at the back to provide

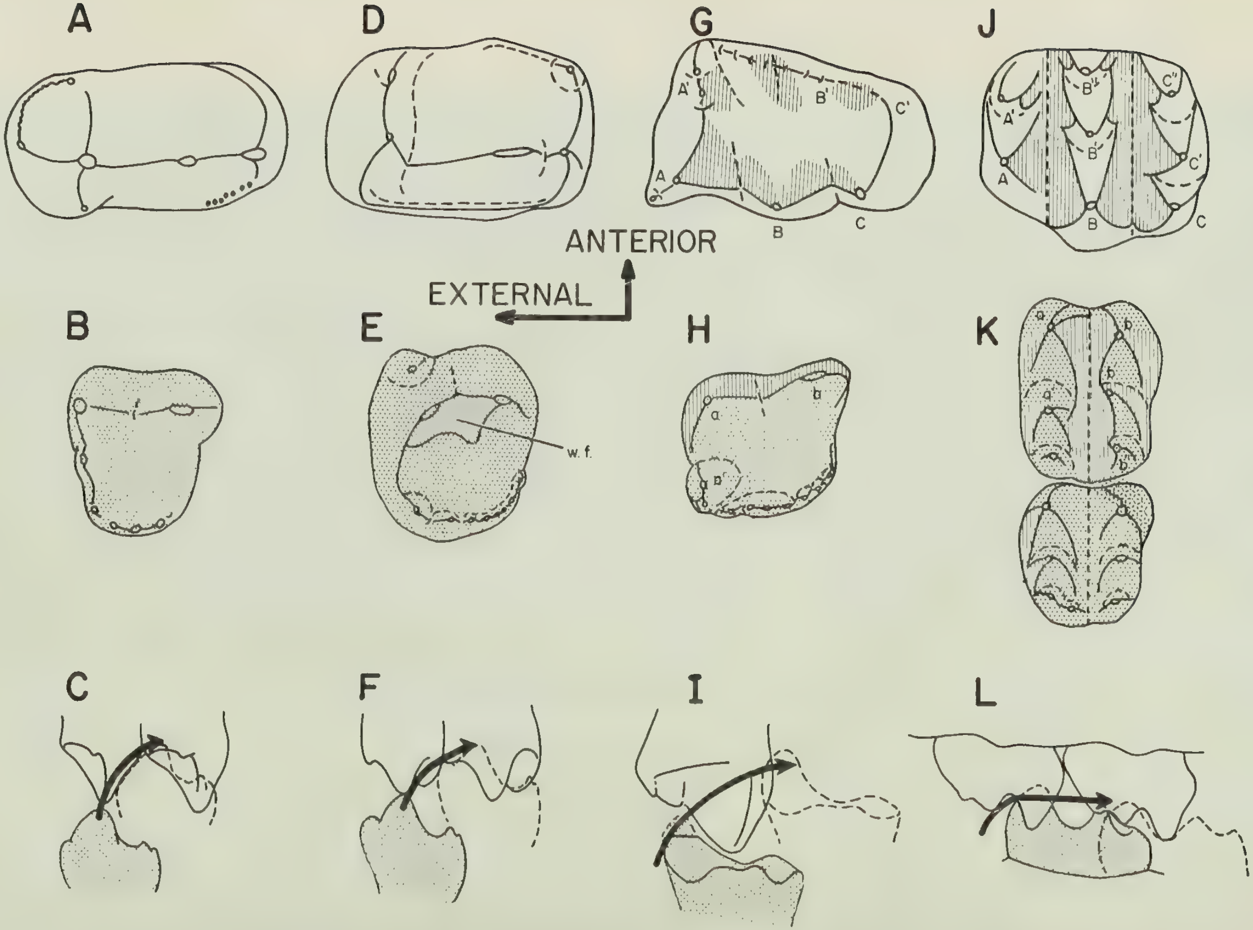

FIG. 13. *Scalenodon angustifrons.* Postcanine teeth. A. Crown view of upper. B. Crown view of lower. C. Lateral view of final stages of dynamic occlusion. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. D. Crown view of upper. E. Crown view of lower. F. Lateral view of final stages of dynamic occlusion. *Massetognathus* sp. (specimen in Yale Peabody Museum). Postcanine teeth. G. Crown view of upper. H. Crown view of lower. I. Lateral view of final stages of dynamic occlusion. *Tritylodon* sp. Postcanine teeth. J. Crown view of upper. K. Crown view of lower. L. Lateral view of final stages of dynamic occlusion.

new shearing surfaces and the loss of worn teeth in front, as well as numerous skull and skeletal features, suggest a close relationship between the tritylodontids and traversodontids. In addition there are several other similarities between the dentitions of individual traversodontids and of *Tritylodon*. These are most marked in *Scalenodon hirschsoni* and the new species of *Massetognathus* described above. In *Tritylodon* and *S. hirschsoni* the rows of postcanine teeth are parallel to the longitudinal axis of the skull and are not arranged obliquely along the edge of the maxilla as in *S. attridgei*, *S. charigi* and earlier cynodonts. The incisors and lower canines of *S. hirschsoni* are procumbent and this, taken together with the parallel postcanine rows, may indicate that there was increased posterior jaw movement during mastication. In *Massetognathus* the postcanine rows are not parallel but there is nevertheless a marked tendency for the rows to be directed away from the edge of the face towards the midline of the skull (Romer, 1967). The nature of the shearing planes between the external surface of the lower postcanines and the internal surface of the external cusps of the upper postcanines was essentially the same in *Tritylodon* and the two traversodontid genera (cf. Fig. 13C, F, I & L). In both *Tritylodon* and the traversodontids lower postcanines occluded with two upper postcanines because of the extensive backward movement of the lower jaw during occlusion. The main difference lies in the presence of the additional cusps of the postcanines in *Tritylodon*. However, cusps that were not present in the more primitive traversodontid *S. angustifrons* (Fig. 13A) were added to the crown of *S. hirschsoni* (13D) and *Massetognathus* (13G).

In these latter animals cusps have been added to the uppers in front of the external and internal main cusps, i.e. in positions which suggest the initial steps in the formation of the external and internal rows of cusps of the tritylodontid upper postcanines. It is significant that the largest cusps of tritylodontid upper postcanines are situated posteriorly and that the anterior cusps decrease progressively in size. The posterior accessory cusps on the external surface of the lower postcanines of traversodontids may also indicate the initial step in the greater development of the external row of cusps typical of tritylodontid lower postcanines. Although the postcanines of *S. hirschsoni* tended to resemble those of tritylodontids it is unlikely that the former reptile was ancestral to the latter; the power stroke was directed forwards in *S. hirschsoni*, whereas it is the backwardly directed power stroke which appears to have characterized *Tritylodon* occlusion. In *Tritylodon* the external and internal rows of cusps of the lower postcanines sheared between the external, central and internal cusps of the corresponding upper postcanines; therefore, if the ancestor of *Tritylodon* were to be found amongst the traversodontids, some indication of this occlusal pattern would be expected in one of the latter. In all the species of *Scalenodon* the transverse ridge of each lower tooth always occluded with the posterior surface of the transverse ridge of the preceding upper tooth; this shows that the lower jaw was not thrust far enough forwards before the power stroke for the transverse ridge of the lowers to be drawn backwards over the transverse ridge of the uppers. In the new species of *Massetognathus* however, the transverse ridges were drawn across one another during occlusion; this appears to be the only known traversodontid where this happened. Neither this species of *Massetognathus* nor *S. hirschsoni* appears to be directly ancestral to the tritylodontids, but, taken together, they show that some traversodontids were developing a postcanine dentition and mandibular movements which were very close to those of tritylodontids. Once two transverse ridges shearing past one another had been developed, it was a relatively simple matter to add more cusps in front of the uppers and behind the lowers, and thus to obtain postcanines of the tritylodontid type. In Fig. 13G & J an attempt has been made to homologise the cusps and regions of the crowns of the upper postcanines of the new species of *Massetognathus* and of *Tritylodon*. The posterior transverse row of cusps has been labelled A, B and C; the second row A^1, B^1 and C^1 and the third row B″ and C″. In Fig. 13H & K the same has been attempted for the lower teeth. It is clear that forms such as *Exaeretodon*, *Gomphodontosuchus* and *S. charigi*, which had lost the central cusp of the upper postcanines, could not have been ancestral to the tritylodontids; neither could forms such as *S. attridgei* with strongly developed anterior masticatory movements.

VII. SUMMARY AND DISCUSSION

The postcanine teeth of all the major groups of cynodonts have been briefly described and figured.

Three new species of traversodontid cynodonts, *Scalenodon hirschsoni*, *S. attridgei* and *S. charigi* have been named and briefly described from their postcanine teeth.

An attempt has been made to trace the evolution of postcanine occlusion in advanced cynodonts. This is shown diagrammatically in Fig. 14. The term occlusion implies that there was tooth-to-tooth contact during the masticatory cycle; the teeth were constructed so that shearing, puncturing and crushing were possible between corresponding upper and lower teeth. Occlusal relationships

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FIG. 14. Origin of the postcanines of *Tritylodon*. For each species the superimposed crown views of upper and lower postcanines are shown next to a posterior view of an occluding pair. Heavy lines indicate the orientation of the shearing planes. White circles indicate the principal cusps of the upper postcanines and black circles the principal cusps of the lower postcanines. Arrows indicate the extent of backward movement, from the beginning of tooth contact to its tightly closed completion. **A.** *Thrinaxodon* sp. Tooth-to-tooth contact did not occur. B. *Trirachodon* sp. C. *Diademodon* sp. Lowers occluded directly with uppers and small shearing surfaces were produced by wear. D. *Scalenodon angustifrons*. Crowns of uppers and lowers were modified to reduce destruction of the tips of the cusps, and transverse elongated shearing surfaces were present. These surfaces came into use as the lower jaw was drawn upwards and backwards. G. *Exaeretodon* sp. A modification of the *S. angustifrons* pattern. *H. Scalenodon hirschsoni* sp. nov. Occlusion involved both an anteriorly directed power stroke and a backwardly directed one. E. *Massetognathus* sp. The transverse shearing surface of the lower postcanines was drawn across the transverse shearing surface of the corresponding uppers (this did not happen in D, G & H above); the transverse shearing surfaces were modified in that small longitudinal shearing surfaces were formed by wear. F. *Tritylodon* sp. The addition of extra cusps, in front of the upper teeth and behind the lowers, increased the length of the longitudinal shearing surfaces (which were comparable to those formed by wear in *Massetognathus*). There were no transverse shearing surfaces. The series from *Diademodon* to *Tritylodon* shows a progressive increase in the extent of the backward movement of the lower jaw during the power stroke.

become progressively more complex within the cynodonts.

In the early cynodonts, the Galesauridae and Procynosuchidae, the lower postcanines bit internal to the uppers, tooth-to-tooth contact between opposing postcanine teeth was not possible and matching shearing planes are therefore absent (Fig. 14A). In both these families replacement of the postcanine teeth was alternate.

In the carnivorous cynodonts, the Cynognathidae and Chiniquodontidae, the lower postcanines still bit internal to the uppers, but matching shearing surfaces are occasionally found on the external surface of the lowers and internal surface of the uppers; this suggests that some form of shearing was possible, but the shearing

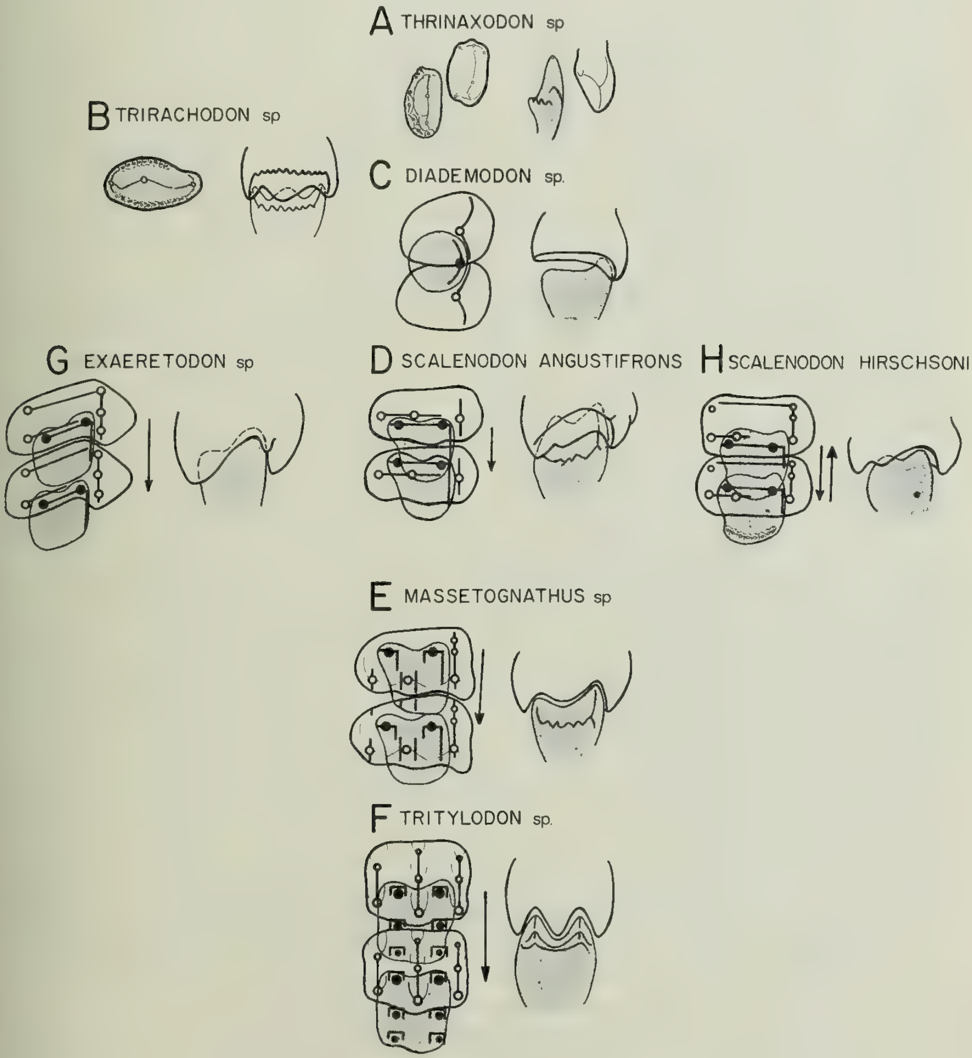
A THRINAXODON sp
B TRIRACHODON sp
C DIADEMODON sp.
G EXAERETODON sp
D SCALENODON ANGUSTIFRONS
H SCALENODON HIRSCHSONI
E MASSETOGNATHUS sp
F TRITYLODON sp.

FIG. 14

mechanism was primitive in comparison with mammalian carnassials and presumably played only a minor role in mastication. Clear-cut alternate replacement of the postcanine teeth was lost.

In the gomphodont cynodonts (Diademodontidae, Trirachodontidae and Traversodontidae) the lower postcanine teeth bit directly against the upper postcanines rather than internal to them. In the Trirachodontidae (Fig. 14B) the transverse ridges of the upper and lower postcanines alternated with one another but complex occlusal patterns were not developed. The crowns of the unworn postcanines of the Diademodontidae were characterized by one or two major cusps and an intricate pattern of smaller cusps and ridges; these were rapidly obliterated by wear so that small matching shearing planes were produced on the outer surface of the main cusp of the lower teeth and the inner surfaces of the main cusp of the uppers (Fig. 14C). However, the main cusp of the lower tooth, because it bit directly against the occlusal surface of the uppers (Fig. 14C), was rapidly worn down; the shearing surfaces can have been effective only for a short time. The continued possession of teeth with vertical shearing surfaces was nevertheless ensured by the addition of new gomphodont and sectorial teeth behind, worn teeth being lost from the front of the postcanine row. As would be expected, there was no alternate tooth replacement; occluding teeth were added sequentially at the end of the row during growth.

The occlusal patterns characterizing the Diademodontidae and closely related forms were refined in the Traversodontidae, where high ridges and deep basins provided effective shearing surfaces. Because the tips of the cusps occluded either opposite basins or externally to matching teeth, they were not worn down as rapidly as in the Diademodontidae. In primitive traversodontids the postcanines did not erupt with accurately matching upper and lower shearing surfaces, but, unlike the teeth of Diademodontidae, they needed relatively little wear of the crown surface to produce them; in *Scalenodon angustifrons* these shearing surfaces were aligned both transversely and longitudinally (Fig. 14D). In order that both these planes could be used effectively during the power stroke of mastication, jaw movements during this phase must have been both upwards and backwards. The transverse ridge which connected the two main cusps of the lower postcanine sheared past the transverse ridge formed by the central and internal cusps of the upper postcanine. The backwardly directed power stroke ended when the transverse ridge of the lower postcanine abutted against the anterior surface of the transverse ridge of the following upper. The arrow in Fig. 14D indicates the extent of this backward movement of a lower postcanine relative to the matching upper postcanine teeth during the power stroke of occlusion.

In a specimen belonging to a new species of *Massetognathus* (Fig. 14E) the basic *Scalenodon* type of postcanine was slightly modified. External cusps were added in front of the external main cusp of the upper postcanines and the longitudinal shearing plane was consequently increased in length. This was apparently coupled with an increase in the length of the backwardly directed component of the power stroke. The two main cusps of the lowers commenced shearing in front of, rather than behind, the transverse ridge of the uppers. As the lower jaw was drawn backwards the lower cusps wore grooves between the internal and central cusps and between the central and external cusps of the uppers; these continued on to the anterior wall of the succeeding upper postcanine. Consequently in the new species of *Massetognathus* what corresponded to the transverse shearing surface of *Scalenodon angustifrons* was broken down into longitudinally orientated shearing surfaces on the sides of the main cusps. As in *Diademodon*, these grooves or shearing surfaces were produced by wearing away a substantial portion of the crown.

In *Tritylodon* (Fig. 14F) these modifications observed in the postcanines of the new species of *Massetognathus* were taken a stage further. The length of the backwardly directed component of the power stroke was increased and cusps were added in front of the upper teeth and behind the lowers. These additional cusps were smaller than the main cusps and they formed two additional transverse rows. Longitudinally orientated shearing planes similar to those which resulted from wear in the new species of *Massetognathus* were present on freshly erupted hardly worn teeth in *Tritylodon*. In *Oligokyphus* an additional row of cusps was added, increasing the length of longitudinally orientated shearing surfaces still further. The entire trend is towards a lengthening of the backward component of the power stroke.

The large South American traversodontids, *Exaeretodon* (Fig. 14G), *Proexaeretodon* and *Ischignathus*, increased the length and height of the vertical shearing surfaces on the internal surfaces of the external main cusps of the upper teeth. The transverse shearing surfaces are obliquely orientated, the central cusp has been lost and a large external cusp added in front of the external main cusp of the uppers. For these reasons it is unlikely that these traversodontids could have been ancestral to the tritylodontids.

In *Scalenodon hirschsoni* (Fig. 14H) and *S. attridgei* wear facets indicate that both longitudinally and transversely orientated shearing planes were present, but, unlike other traversodontids, they could make both forwardly and backwardly directed power strokes during mastication.

The postcanine teeth of traversodontids and the tribosphenic molars of primitive mammals functioned in similar ways. Both have shearing surfaces on the vertical faces of the main cusps and both had jaw movements during the final stages of the masticatory cycle which were not directly orthal; in primitive therian mammals the power stroke had a marked transverse component (Crompton & Hiiemäe 1969*a* & *b*), while in traversodontids it had a strong posterior component. These movements in the horizontal plane permitted several shearing surfaces to be used as the jaws were closed.

In traversodontids but not in the tritylodontids the mandibular symphysis was massive and presumably immobile during life. The left and right lower postcanine teeth were slightly further apart than the corresponding upper postcanines; the opposite is true of primitive mammals. These two characters of traversodontids suggest that during the final stages of mastication both mandibular rami were drawn directly backwards and occlusion had to occur on both sides simultaneously; the greater the extent of the backward movement the more nearly parallel the rows of postcanine teeth. This is not possible in a primitive mammal (Crompton & Hiiemäe, 1969*a* & *b*). Significant transverse mandibular movements in cynodonts and tritylodontids were prevented by the massive transverse processes of the pterygoid bones and the structure of the postcanine teeth. The structure of the lower jaw of primitive mammals (Crompton 1963, Krebs 1969) suggests that remnants of the transverse processes of the pterygoids may have been present in some cases; it is possible that their reduction in early mammals was coupled with changes in jaw musculature permitting the introduction and strengthening of transverse mandibular movements.

The mechanism involved in developing occlusion in gomphodont cynodonts and in mammals (Crompton & Jenkins, 1968) appear to have been similar. In the early forms of both groups the crowns of corresponding upper and lower teeth were shaped by wear to produce matching shearing planes; in both a complex series of cusps and ridges had to be obliterated by wear before the teeth could function efficiently. This is particularly true of the cynodont *Diademodon*, of the new species of *Massetognathus* and of the mammal *Eozostrodon* (=*Morganucodon*). In the later traversodontids, tritylodontids and mammals the postcanines and molars lacked superfluous crown structures that had to be worn down and the crowns already possessed shearing planes that were genetically determined rather than produced by wear. The numerous Middle Triassic cynodonts from South America and the abundant early mammal teeth should be studied in detail in order to clarify further this aspect of evolutionary change.

The distribution of traversodontid cynodonts is briefly discussed; it suggests ready access between the continental masses of Africa and of South America during the Trias. The Traversodontidae may nevertheless have had a worldwide distribution.

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ABBREVIATIONS USED IN TEXT-FIGURES

a.a.c.l.	anterior accessory cusp of lower postcanine
a.a.c.u.	anterior accessory cusp of upper postcanine
a.r.	anterior ridge
a.v.	anterior valley
a.w.	anterior wall
b.l.	basin in lower postcanine
b.u.	basin in upper postcanine
c.c.u.	central cusp of upper postcanine
e.	embayment
e.cing.	external cingulum
e.c.l.	external cusp of lower postcanine
e.c.u.	external cusp of upper postcanine
en.	enamel
i.c.l.	internal cusp of lower postcanine
i.c.u.	internal cusp of upper postcanine
p.a.c.	posterior accessory cusp
p.b.	posterior basin
p.c.	posterior cingulum
p.r.	posterior ridge
p.v.	posterior valley
p.w.f.	postcanine wear facet
s.	saddle
Sh.s.	shearing surface
t.r.	transverse ridge
t.r.l.	transverse ridge of lower postcanine
t.r.u.	transverse ridge of upper postcanine
w.f.	wear facet.

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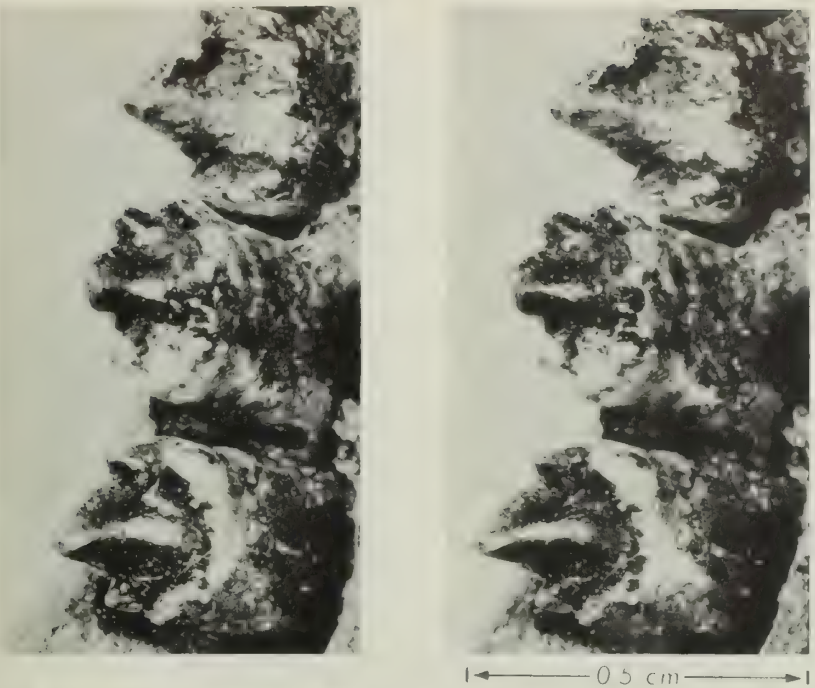
PLATE 1

Thrinaxodon liorhinus

A. Oblique internal view of last three left lower postcanines.
B. Oblique internal view of last five left upper postcanines.

A



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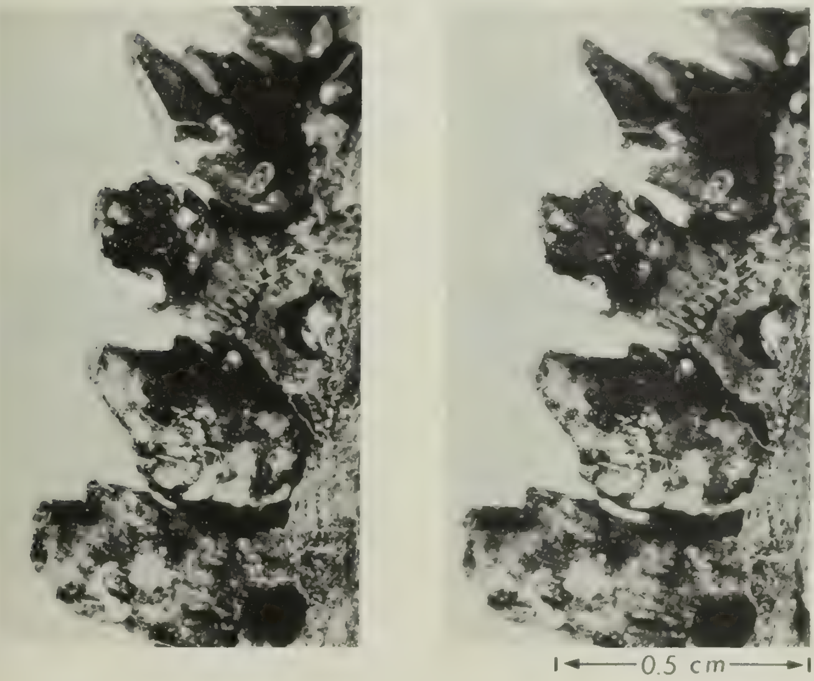
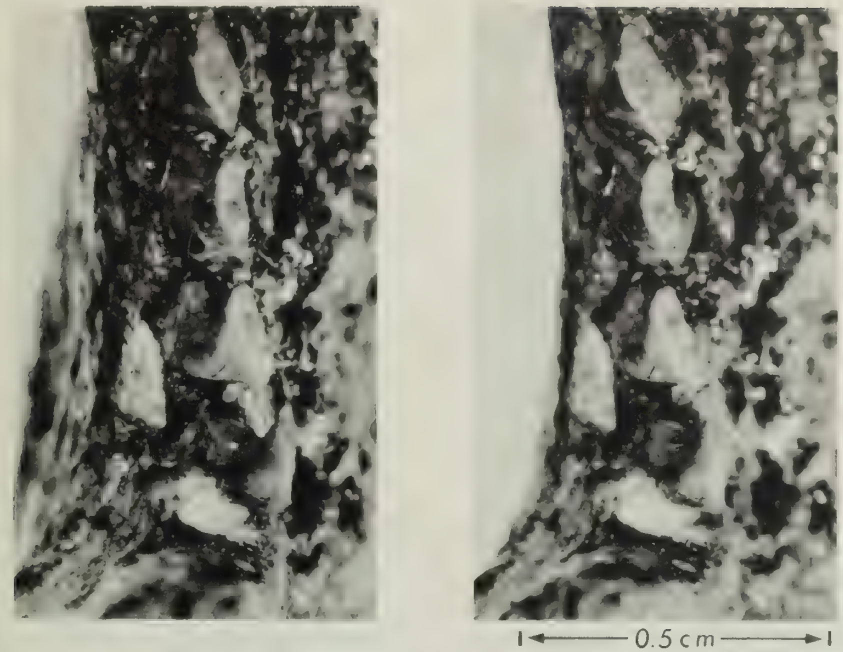


PLATE 2

A. ***Glochinodontoides gracilis*** (holotype, American Museum of Natural History, no. 2223). Crown view of first four left upper postcanines.

B. ***Diademodon*** sp. (Bernard Price Institute, Johannesburg, no. 1675). Crown view of isolated postcanines; all except centre right are uppers.

A



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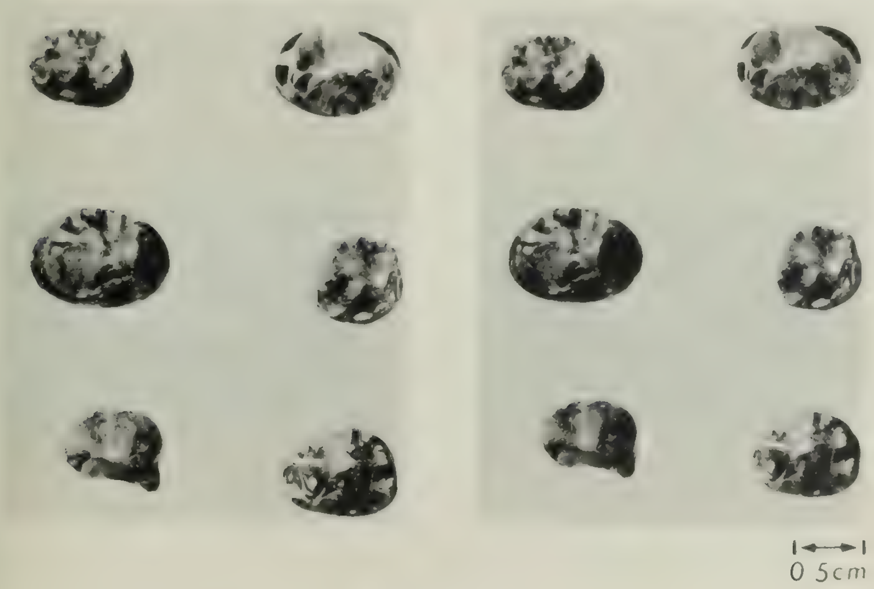


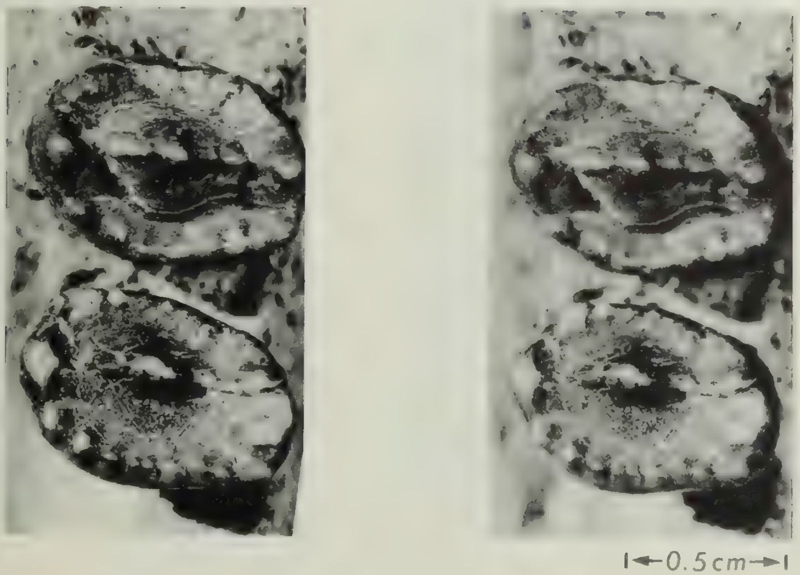
PLATE 3

Cricodon metabolus (holotype, Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 74).

A. Crown view of 7th and 8th right lower postcanines.

B. Crown view of 7th right upper postcanine.

A



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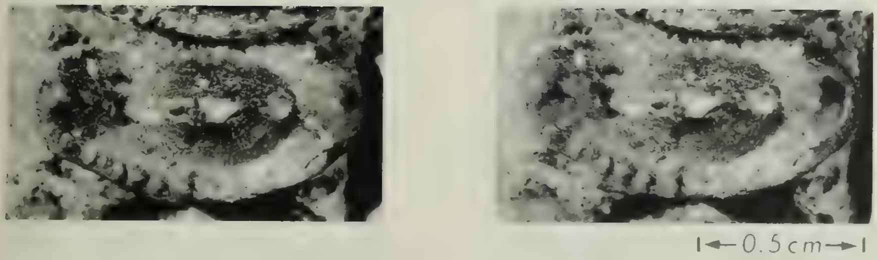


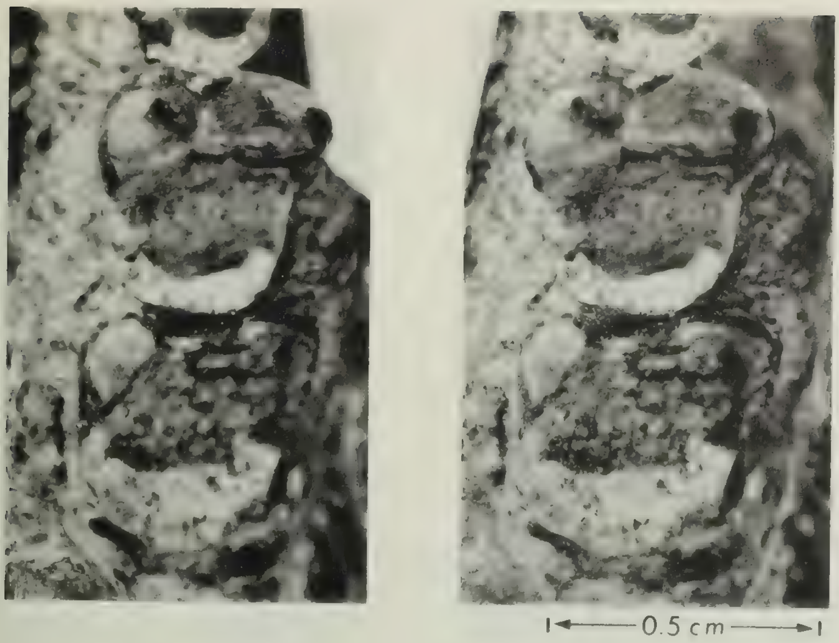
PLATE 4

Scalenodon angustifrons (holotype, Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 120B).

A. Crown view of last two left lower postcanines.

B. Crown view of last three right upper postcanines.

A



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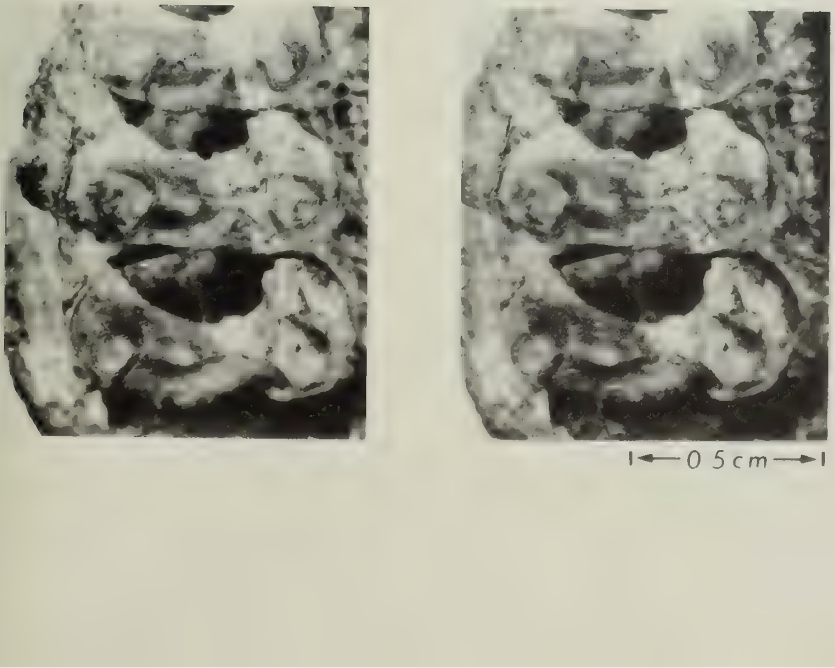


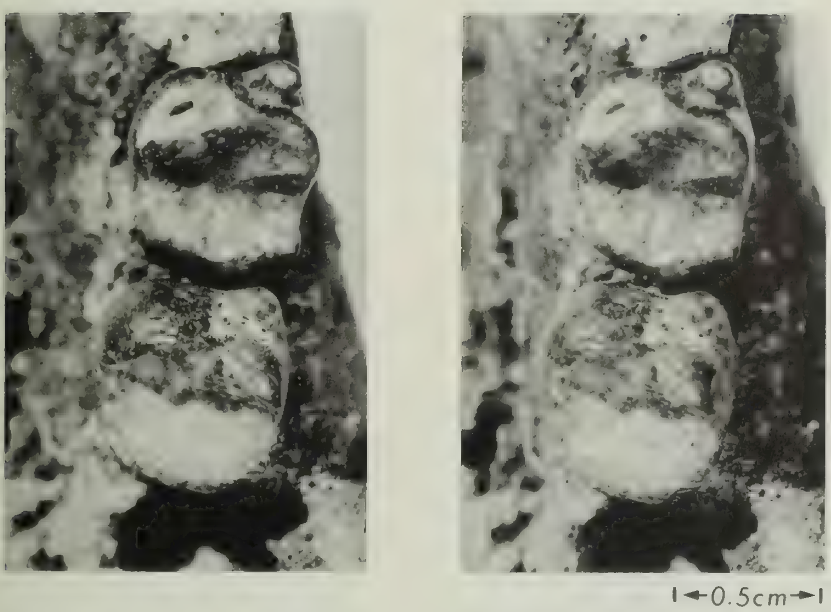
PLATE 5

Scalenodon hirschsoni sp. nov. (holotype, B.M.(N.H.) no. R. 8577).

A. Crown view of 5th and 6th right lower postcanines.

B. Crown view of 5th right upper postcanine.

A



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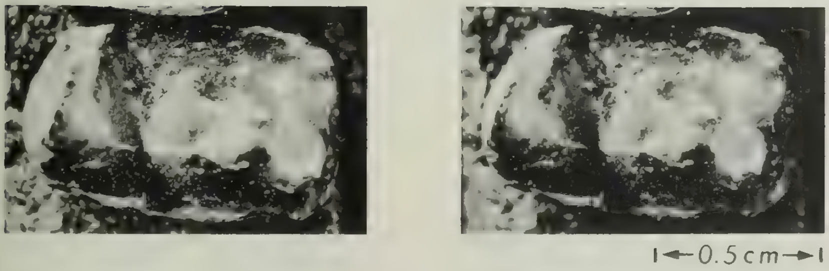


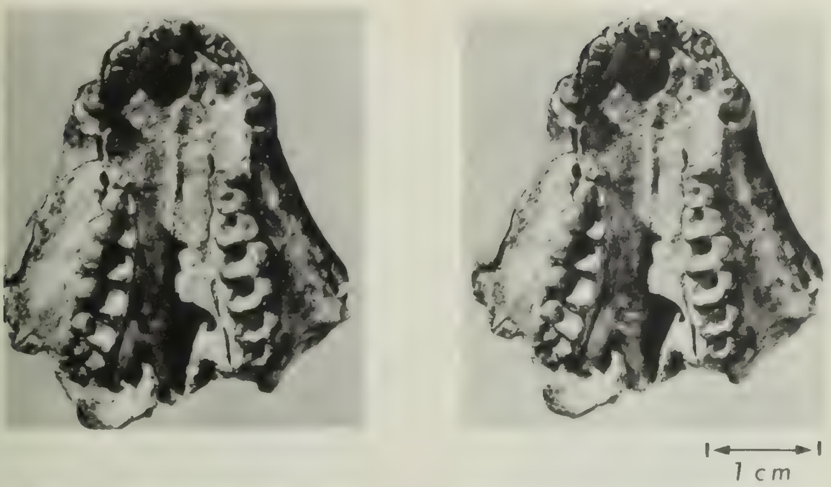
PLATE 6

Scalenodon attridgei sp. nov. (holotype, B.M.(N.H.) no. R.8578).

A. Entire palate.

B. Crown view of right upper postcanines.

A



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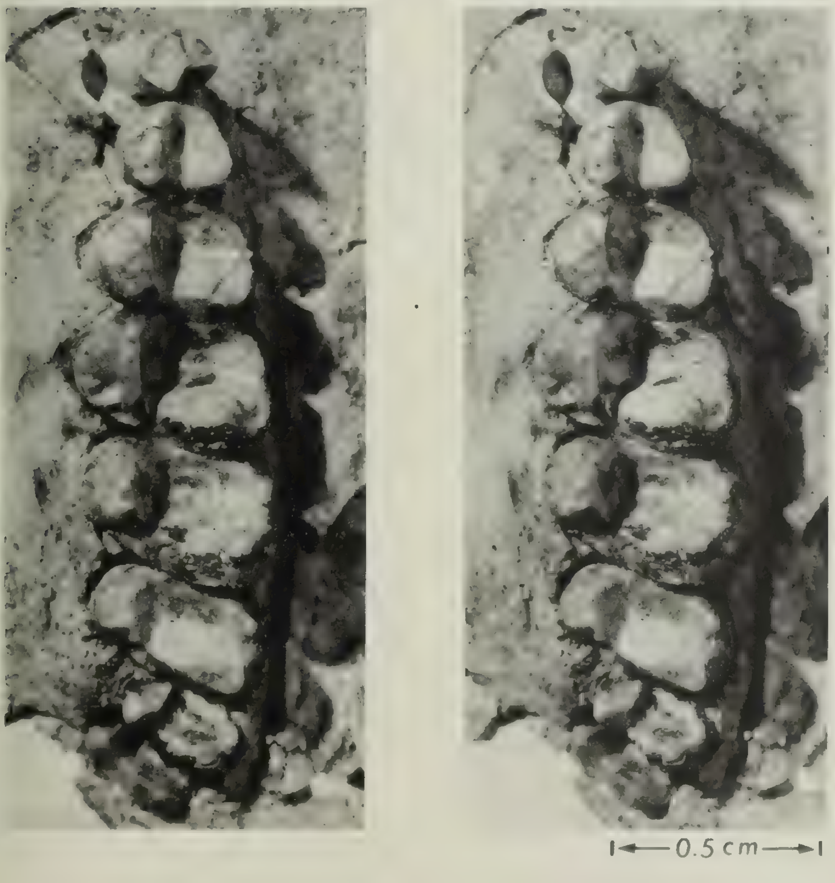


PLATE 7

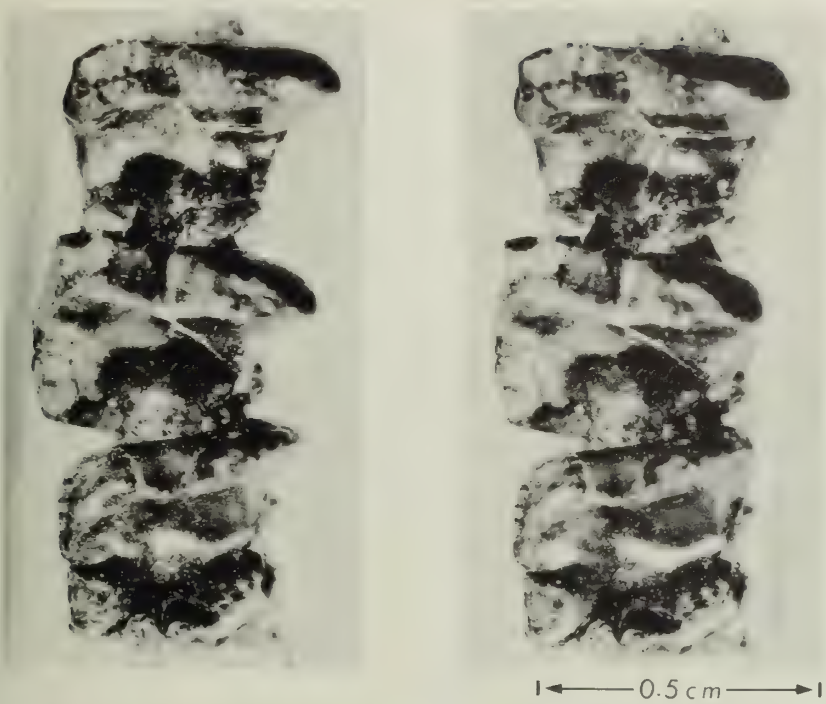
Massetognathus sp. (Yale Peabody Museum).

Matching upper and lower postcanines.

A. Crown views of 3rd, 4th and 5th left lower postcanines.

B. Crown views of 3rd, 4th and 5th left upper postcanines.

A



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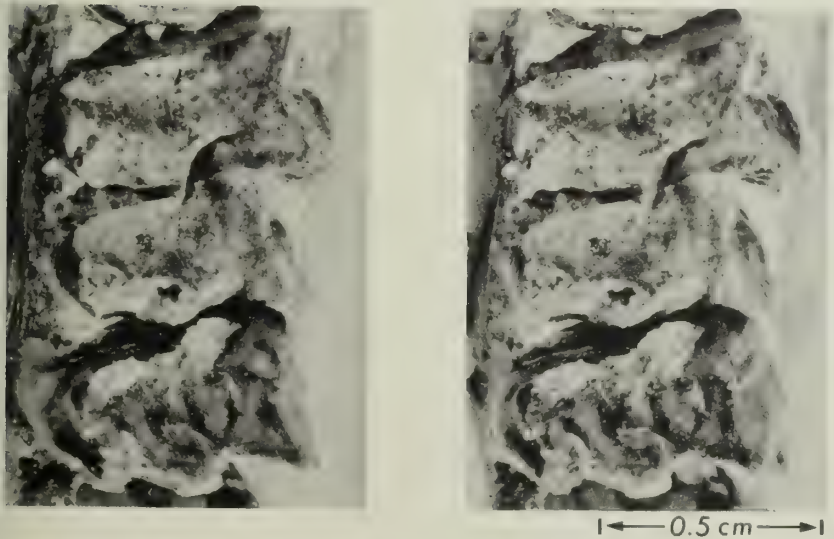

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THE LOWER MIOCENE RUMINANTS OF GEBEL ZELTEN, LIBYA

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W. R. HAMILTON

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THE LOWER MIOCENE RUMINANTS OF GEBEL ZELTEN, LIBYA

BRITISH MUSEUM
8 JUN 1973
NATURAL HISTORY

BY

WILLIAM ROGER HAMILTON

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THE LOWER MIOCENE RUMINANTS OF GEBEL ZELTEN, LIBYA

By W. R. HAMILTON

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SYNOPSIS

RUMINANTS from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya, are described. The skull and dentition of a new giraffoid—*Zarafa zelteni*— are described in detail. This genus exhibits dental characteristics which ally it to the palaeomerycids; however details of the cranial anatomy indicate a close relationship to the palaeotragines. *Zarafa* is classified as a palaeotragine and its palaeomerycid features are interpreted as evidence of a common ancestry for the two groups. The Palaeotraginae and Giraffinae are grouped in the Giraffidae.

The skull and dentition of *Prolibytherium magnieri* indicate that it is a member of the Sivatheriidae and primitive features of the skull suggest the divergence of the two families soon after the origin of the Giraffoidea in the late Oligocene.

The different evolutionary trends exhibited by the Giraffidae and the Sivatheriidae are related to the different fighting methods used in intra-specific combat. In the Giraffidae an elongation of the neck and limbs was possible while in the Sivatheriidae selective pressures existed tending to maintain the short neck and limbs.

The other Gebel Zelten ruminants are poorly represented but a new genus and species—*Canthumeryx sirtensis*—is described and identified as a palaeomerycid. A new tragulid species—*Dorcatherium libiensis* and three bovid species—*Gazella sp.*, *Protragocerus sp.* and *Eotragus sp.* are present in the fauna.

A further study of the ruminants from the Miocene of East Africa, enables the species *Palaeomeryx africanus* and *Walangania gracilis* to be synonymized as *Walangania africanus* and the upper dentition of *Propalaeoryx nyanzae* is described. A new species—*Gelocus whitworthi*—is described, this is the first recorded occurrence of the Gelocidae in Africa.

The influence of these new discoveries upon the accepted classification of the giraffoids is discussed.

I. INTRODUCTION

The fossil vertebrate fauna of Gebel Zelten, Libya was discovered by Arambourg (1961a and b) who published preliminary notes on some new elements in the fauna. Further collections were made by R. J. G. Savage of Bristol University between 1964 and 1968. Many crania of *Prolibytherium magnieri* were collected and as some of these were of superior quality to the holotype, described by Arambourg (1961a); a full and detailed study of this species has been made. The presence of a second giraffoid—*Zarafa zelteni*—was not known until 1968 when M. White of Bristol University, completed the preparation of a skull which had been discovered, enclosed in a sandstone block. These two species form the basis of this work but as the study proceeded its scope was expanded to include the other ruminants of the area and finally a revision of some elements of the East African Miocene fauna was made.

Gebel Zelten

Gebel Zelten lies about 200 km south of the Gulf of Sirte, Libya. It consists of an elongate mesa running northwest-southeast for about 140 km at 19° 30′–20° 30′E. 28°–29°N. The ESSO Company oil camp of Zelten lies to the north of the gebel and the Oasis Oil Company of Libya camp lies to the south; the road between these camps crosses the gebel at its narrowest point where it is only 8 km. wide. In the west the gebel rises 40–60 m above the Zelten Rambla; it dips gently to the east and blends with the Calenscio Serir at its eastern end. The plateau is capped by marine sandstone which is Lower Miocene in age and the edges are dissected by steep walled wadis up to 3 km in length (Savage and White 1965). It is in these wadis that many of the vertebrate remains are found though some of the sites are on areas of washout from the wadis.

Detailed geological studies of the area have been published by Magnier (1962) and Selley (1968 and 1969); a detailed study of the geology with reference to the vertebrate sites is in preparation (Savage pers. comm.). The vertebrate remains are found in fluviatile deposits which probably originated in a coastal, alluvial flood plain (Selley 1969). The conditions at the time of deposition are interpreted as those of the savannah by Desio (1935) and again by Savage and White (1965).

Desio (1935) indicated that the Zelten deposits are Burdigalian and Helvetian in age and he stated that the deposits on the south side of Gebel Zelten are of Aquitanian age. Arambourg and Magnier (1961) and Arambourg (1961a and b, 1963a and b.) have consistently placed the deposits in the Burdigalian, and Arambourg (1963b) states that the Gebel Zelten deposits rest on Oligocene marine beds and are overlain by Helvetian marine beds. Savage and White (1965) indicate a Burdigalian age and this was later refined (Savage in Selley 1969) to Early Burdigalian or Late Aquitanian.

Terminology

In most anatomical details the terminology used follows that of Sisson and Grossman (1953). The nomenclature applied to the dentition (Text fig. 1) is mainly after Arambourg (1947). In the upper molars the postero-lingual cusp, termed the hypocone by Arambourg (1947) is here termed the metaconule after Weber (1928). In the lower molars I have treated the antero-lingual corner as if the paraconid has been entirely lost, thus the antero-lingual cuspid is the metaconid with an anterior mesostylid. The '*Palaeomeryx* fold' is used to define any fold of enamel which runs vertically down the postero-labial face of the protoconid into the median valley.

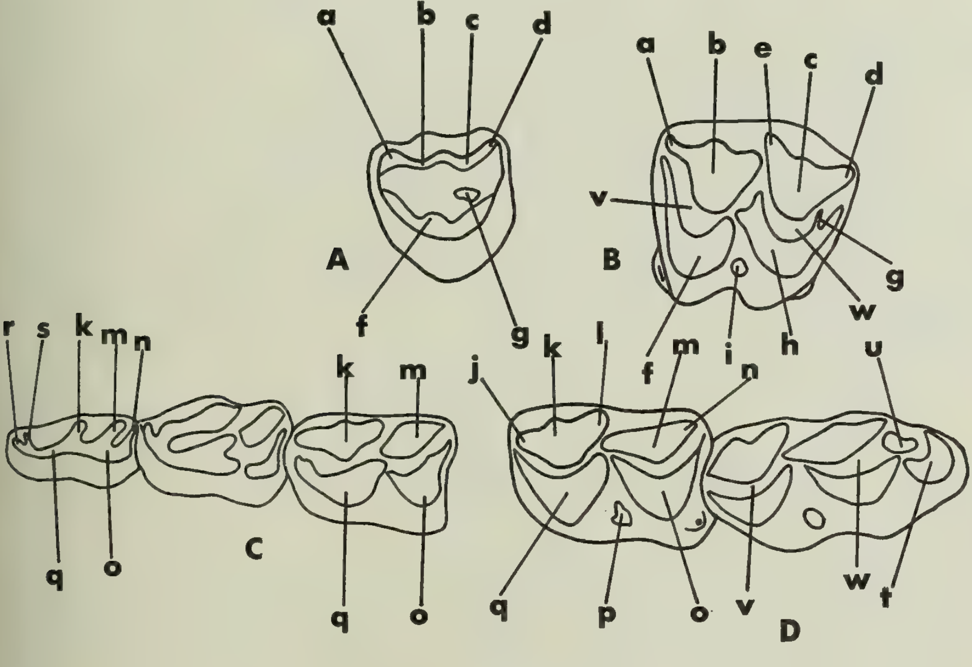

Fig. 1. Ruminant molar and premolar cusp nomenclature. (A) Third upper premolar. (B) First upper molar. (C) Second, third and fourth lower premolars. (D) Second and third lower molars. *Upper dentition.* a: parastyle. b: paracone. c: metacone. d: metastyle. e: mesostyle. f: protocone. g: accessory crest. h: metaconule. i: entostyle. *Lower dentition.* j: mesostylid. k: metaconid. l: metastylid. m: entoconid. n: entostylid. o: hypoconid. p: ectostylid. q: protoconid. r: parastylid. s: paraconid. t: hypoconulid. u: entoconulid. v: anterior fossette. w: posterior fossette.

The abbreviations used in reference to the dentition follow the convention in general use in Britain and America. I, C, P and M represent incisor, canine, premolar and molar respectively; the tooth is then defined by a number added above or below the line to indicate presence in the upper or lower jaw; thus P_4 is the lower, fourth premolar which is in contact with M_1 the first lower molar. The deciduous cheek teeth are referred to as D^1, D_1 etc. The external side of the tooth is labial and the internal side is lingual. Anterior and posterior with reference to the dentition, indicate those directions which apply if the mandible or maxilla is in the horizontal position.

Frontal Appendages

In current usage the term 'horn' can refer to any cranial appendage but in this work a restriction of the term is applied. In the ruminants the type of frontal appendage is some times the main criterion on which the classification of a genus is based as stated by Pilgrim (1941):

> '. . . the varying types of frontal appendage—horns—constitute one of the most important distinctions between the different families of the Pecora.'

In this situation it is clearly desirable that separate terms be applied to the different types of frontal appendage. Voorhies (1969) listed four types of frontal appendages in the living artiodactyls as:

> '1. the unshed true horns growing on the bony core in the Bovidae, 2. the deciduous antlers of the Cervidae, 3. the annually-shed horny sheath growing over a permanent, vascular bony core in the Antilocaprinae, and 4. the bony core permanently covered by skin ('velvet') in the Giraffidae.'

The first three of these appendages are referred to as; 'horns', 'antlers' and 'horn-cores' respectively but no widely accepted term exists for the giraffid appendage. Lankester (1907) used the term 'ossicone' to refer to this appendage and defined ossicones as:

> '. . . independently ossifying bony cores which are found in *Okapia* and *Giraffa* on the frontal and parietal areas and in the giraffe also in the median position.'

A slight widening of the application of this term was made by Ginsburg and Heintz (1966) who applied the term to the palaeomerycid appendage and its application to all giraffoid cranial appendages is desirable.

Abbreviations

The prefix 'M' refers to specimens in the collections of the British Museum of Natural History, London: 'B.U.' in the Department of Geology, University of Bristol and 'P' in the Institut de Paléontologie, Paris. Specimens described in chapter 4 are the property of the National Museum, Nairobi, Kenya and are defined by the prefix 'K'.

Classification

The system of classification used in this work differs slightly from that of Simpson (1945), this is mainly due to alterations within the Giraffoidea and primitive Cervoidea. The Palaeomerycidae is treated as a family of the Giraffoidea and following the suggestion of Ginsburg and Heintz (1966), those genera of the family Palaeomerycidae which lack frontal appendages, are removed to the separate family Dremotheriidae. The family Blastomerycidae is grouped with the Dremotheriidae in the Dremotherioidea. The position of the Dromomerycidae is uncertain and requires further study, but in this work the family is treated as a group probably originating in the nearctic region and having no direct relationship to the Palaeomerycidae.

The family Giraffidae has been split by the establishment of the Sivatheriidae as a separate family.

ACKNOWLEDGEMENTS

I would like to express my deepest thanks to all those who have helped in making this work possible. Dr. R. J. G. Savage suggested the topic and by his encouragement, advice and friendship, he has contributed much towards its completion. The technical staff of the Department of Geology, University of Bristol, have all helped and I would particularly like to thank Mr. M. White for his work in preparation of the material and Mr. R. Godwin who prepared the plates.

I would like to thank the staffs of the museums that I have visited. Professor M. Crusafont Pairo of Sabadelle, Spain and Professor Lehman of l'Institut de Paléontologie, Paris; have allowed me access to the collections and provided facilities for study. Dr. A. Sutcliffe of the British Museum of Natural History, allowed me to use the collections and facilities and the Keepers of palaeontology and zoology extended facilities on which I borrowed material.

Dr. L. S. B. Leakey allowed me to study and redescribe the ruminant material from Kenya and Dr. A. W. Gentry gave advice and comment on the intricacies of bovid classification. Dr. Churcher provided up to date information on his study of the East African giraffids which helped to avoid any overlap in our studies.

This study was carried out under a N.E.R.C. Research Studentship and the University of Bristol provided me with facilities during the tenure of this studentship from 1967 to 1970.

II. SYSTEMATIC DESCRIPTIONS

Family **TRAGULIDAE** Milne-Edwards 1864

Diagnosis: Small primitive ruminants; lacking frontal appendages. Dentition primitive but with upper incisors reduced or absent. Upper canines large, especially in the male. Molars bunodont but showing selenodonty in advanced forms. Limbs showing features of advanced ruminants but with varying degrees of fusion exhibited by the metacarpals and metatarsals. Navicular and cuboid fused. (After Milne-Edwards 1864).

Genus ***DORCATHERIUM*** Kaup 1833

Diagnosis: This genus was defined by Whitworth (1958 p. 3) whose diagnosis is followed here.

Type species: *Dorcatherium naui* Kaup 1833.

Dorcatherium libiensis sp. nov.

DIAGNOSIS: A small species of *Dorcatherium*. Length of lower tooth row P_3–M_3 about 39 mm.

REMARKS: This species is established on a size basis and further work in the Gebel Zelten area may reveal wide variation in the species; however as the species is very rare at Gebel Zelten and as collecting in the area has been terminated it was decided, with some hesitancy, to establish the species on the basis of a single specimen.

HOLOTYPE: M.26684. A fragmentary right mandible with P_3 to M_2 and the alveoli of P_1 and P_2 preserved.

LOCALITY: The Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

Lower Dentition. The molars are heavily worn but the main details of their anatomy are visible (pl. 1, fig. 1). M_1 is complete though badly cracked posterior to the median valley and the postero-lingual corner of M_2 is missing. The molars are bunodont as in *D. chappuisi* and *D. naui* and strong anterior and posterior cingula were present on M_1 and M_2. The posterior face of the protoconid bears a strong fold similar to a '*Palaeomeryx* fold' but more lingually situated and similar to that of *D. chappuisi*. The postero-lingual region of the metaconid carries a deep vertical groove on both molars, as in *D. naui* and *D. chappuisi* this fold seems to be characteristic of the genus *Dorcatherium*. A small ectostylid is present in the median valley as in *D. naui*, this stylid is usually absent in *D. chappuisi*.

The anterior end of P_3 is missing but P_4 is complete. The premolars are elongate and similar to those of *D. chappuisi* and *D. naui*. The dentition of *D. libiensis* is thus similar to that of *D. chappuisi* and is distinguished from this species and *D. pigotti* on a size basis only.

The presence of this mandible in the Gebel Zelten fauna serves to establish the presence of the genus in North Africa at this time but gives no indication of the relative abundance of tragulids at Gebel Zelten, as specimens of this size and smaller, are relatively rare in the collection (Savage and White 1965).

TABLE 1

	D. libiensis M.26684		*D. chappuisi* (Whitworth)		*D. pigotti* (Whitworth)	
	Length	Width	Length	Width	Length	Width
P_3	10·0 mm	3·6 mm	13·5 mm	5·1 mm	8·4 mm	3·1 mm
P_4	9·6 mm	4·0 mm	12·3 mm	6·0 mm	7·9 mm	3·8 mm
M_1	9·3 mm	5·8 mm	11·7 mm	7·2 mm	8·2 mm	4·8 mm
M_2	11·0 mm	6·6 mm	12·9 mm	9·0 mm	8·9 mm	5·3 mm

Superfamily **GIRAFFOIDEA** Simpson 1931

DIAGNOSIS: Medium to large sized ruminants. Cheek teeth brachyodont or occasionally hypso-brachyodont. Enamel of cheek teeth usually rugose. Ossicones present in male and sometimes female. Metapodials fully fused.

Comments: This is a well defined group of ruminants which is probably related more closely to the Cervoidea than the Bovoidea and is in many respects more primitive than either group.

Family **PALAEOMERYCIDAE** Lydekker 1883

Diagnosis: A group of primitive giraffoids exhibiting features that may indicate a close relationship to the cervoids. Ossicones are present and in some species these have a long proximal region and a whorl of short tines distally. The mandible is shallow with brachyodont selenodont molars which have lightly rugose enamel. P_1 may be present. Metastylid and entostylid usually very prominent and strong cingula are present anteriorly and posteriorly. A '*Palaeomeryx* fold' is often present. Labial ribs of the upper molars prominent. Accessory crests often present in the fossettes and entostyle usually present in the median valley.

Genus ***CANTHUMERYX*** nov.

Diagnosis: A medium sized ruminant, about as large as the fallow deer, *Dama dama*. Lower dentition similar to *Propalaeoryx* but lacking P_1. Lower molars relatively high with weaker mesostylid and a stronger more flexed metastylid than is usual in the palaeomerycids. Strong anterior and weak posterior cingula on M_1 and M_2. Premolars elongate similar to usual palaeomerycid pattern but strong entostylid on P_4.

Type species: *Canthumeryx sirtensis* sp. nov.

Diagnosis: As for genus.

Derivation of name: The generic name is from Canthus a character of Greek mythology: according to Appollonius:

> 'Fate had decreed that he and the great seer Mopsus should wander to the ends of Libya to be destroyed.' (Rieu 1959).

The trivial name refers to the Sirte basin in which the specimens were discovered.

Holotype: A mandibular fragment with D_3 to M_3, the last molar being only partially erupted. M_3, P_4 and P_2 have been dissected out.

Locality: The Lower Miocene (Burdigalian) of Gebel Zelten, Libya.

Material:

M.26682	Holotype.
M.26683	A right mandibular fragment with D_4 and M_1 erupted. P_3 and P_4 dissected out.
B.U.20111	An isolated lower right M_3 showing moderate wear.

Lower Dentition. The lower dentition forms a closed series from P_2 to M_3 and P_1 is absent as in *Palaeomeryx* but in contrast to *Propalaeoryx*. The enamel of the molars is finely rugose and the molars are higher and more elongate than in *Palaeo-*

meryx but lower and slightly wider than in *Propalaeoryx*. The metaconid of M_1 is transversely flattened with a weak mesostylid, a strong lingual rib and a strong metastylid which is flexed more lingually than in *Palaeomeryx* and is longer and more slender than in *Propalaeoryx*. The entoconid has a strong lingual rib, the cuspid is almost parallel to the axis of the molar as in *Propalaeoryx* whereas in *Palaeomeryx* it has a more diagonal orientation. The posterior end of the entoconid is reduced and rounded in M_1 (pl. 1, fig. 2). The hypoconid is isolated until very late in wear and the anterior fossette would be entirely worn away before the hypoconid wear trace joined that of the protoconid. The hypoconid is much lower than the protoconid, but due to the increased overall height of the tooth, this difference is less marked than in *Palaeomeryx*. The posterior end of the hypoconid is produced lingually forming the posterior end of the tooth and causing the posterior fossette to open lingually in M_1 (pl. 1, fig. 3).

M_2 is very similar to M_1 but the posterior end of the entoconid bears a strong keel, causing it to extend further posteriorly and tending to close the posterior fossette which opens at the postero-lingual corner of the tooth; this contrasts with *Propalaeoryx* in which the entoconid of M_2 is rounded posteriorly and the posterior fossette opens lingually as in M_1. In *Palaeomeryx* the posterior end of the entoconid usually bears a strong crest in M_1 and M_2.

M_3 has a feeble mesostylid and a strong metastylid. The entoconid is transversely flattened and its anterior region consists of a strong crest of enamel which meets the anterior face of the protoconid. The posterior region of the entoconid consists of a strong crest and from its posterior end the long mentoconulid curves posterolabially, to blend into the middle of the lingual face of the hypoconulid. The protoconid joins the posterior end of the metaconid closing the fossette even in the unerupted condition; this region is very variable in *Palaeomeryx* but in *Propalaeoryx* it is similar to *Canthumeryx*. The posterior end of the hypoconid is short, it meets the hypoconulid but fails to reach the entoconulid. The crescentic hypoconulid is lower than the hypoconid. The molars each have a strong ectostylid in the median valley (pl. 1, fig. 4) and M_3 has a small stylid in the posterior valley. A strong anterior cingulum is present on each molar and feeble posterior cingula are present on M_1 and M_2.

The P_4 of *Canthumeryx* is generally similar to that of *Palaeomeryx* or *Propalaeoryx*. The metaconid is the highest part of the tooth, it is strongly swollen anteriorly (pl. 1, fig. 5) and produces a strong wing posteriorly, these features are similar in *Palaeomeryx* but in *Propalaeoryx* the anterior and posterior projections are absent. The protoconid is joined to the metaconid by a strong ridge of enamel as in *Palaeomeryx*. The entostylid is very strong in *Canthumeryx* (pl. 1, fig. 5), curving across the whole posterior face of the tooth as in *Propalaeoryx* and in contrast to *Palaeomeryx* in which it is reduced lingually. The entoconid of *Palaeomeryx* usually curves posterolingually at its lingual end but there is no indication of such a curvature in *Canthumeryx* or *Propalaeoryx*. The paraconid and parastylid are very strong and widely divided in *Canthumeryx* (pl. 1, fig. 5) and *Propalaeoryx* whereas in *Palaeomeryx* they are usually weaker and less widely divided. The labial face of the P_4 is swollen labially in *Palaeomeryx* but in *Canthumeryx* and *Propalaeoryx* this swelling is absent and the wall is vertical. A strong groove on the labial wall separates the hypoconid from the protoconid, this groove is very strong in *Palaeomeryx* weaker in *Canthumeryx* and weaker again in *Propalaeoryx.*

P_3 is more elongate than P_4; the metaconid is lower than in P_4 and it has no posterior fold or anterior swelling, it is also situated further posteriorly than on the P_4 (pl. 1, fig. 5). The posterior region consists of a hypoconid and an entoconid as in the P_4 but the entostylid is joined to the posterior face of the entoconid from which it curves postero-lingually and does not join the hypoconid (pl. 1, fig. 5); this is probably an individual variation which is also found in *Palaeomeryx* and *Walangania* and in these genera it is more usual for the posterior region of the P_3 to resemble that of the P_4.

The P_2 of *Canthumeryx* is relatively simple with a single, conical, primary cuspid in the central region from which an unforked anterior crest is produced; this curves lingually at its anterior end. A posterior swelling and a postero-lingual crest are produced from the primary cuspid. The posterior region is much lower than the primary cuspid, it consists of a single transverse crest which falls away posteriorly. Strong anterior and posterior cingula are present on all the premolars.

The D_4 is heavily worn in both specimens. It is elongate and trilobed; its anterior end is narrower than the posterior end and the anterior, median and posterior fossettes are joined (pl. 1, fig. 2). The anterior fossette is bounded by a strong labial cuspid and a narrow lingual cuspid, the anterior end is closed by a small stylid. In both specimens the anterior region is very heavily worn and very little surface detail is visible. The metaconid is high and selenodont as in the molars (pl. 1, fig. 2), it has a strong metastylid which communicates with the high entoconid.

The posterior region of the entoconid is shortened as in the M_1 and the posterior fossette opens lingually (pl. 1, fig. 2). The protoconid is stout and crescentic, in the heavily worn condition its wear trace is joined to the antero-labial cuspid. The hypoconid is higher than the protoconid but this may be a wear factor. The D_4 has a very strong ectostylid in the median valley. The posterior cingulum is strong and the anterior cingulum continues along the labial face as far as the anterior valley, in which there is a weak cingulum.

The D_3 is elongate narrowing anteriorly. The primary cuspid lies in the middle of the tooth and has a feeble lingual cuspid. The anterior region is similar to that of P_3 with a long crest giving rise to antero-lingual and lingual branches. The posterior region has a single central hypoconid which is joined by a crest to the primary cuspid. The hypoconid produces a posterior branch which curves lingually at its posterior end and a lingual branch which curves posteriorly, a large enamel island is produced between these branches.

The D_2 is known from the alveoli only (pl. 1, fig. 4); these are single, anterior and posterior and indicate that D_2 was slightly less elongate than the D_3. The absence of a D_1 indicates that P_1 was also absent.

The dentition of *Canthumeryx* resembles that of *Propalaeoryx* more closely than any other ruminant, and both resemble *Palaeomeryx.* Differences of the metastylid, entoconid, height and width serve to distinguish the molars of *Canthumeryx* from those of *Palaeomeryx* and *Propalaeoryx* and many details of the fourth premolars present differences between these genera. The absence of a P_1 in *Canthumeryx* is an important difference distinguishing it from *Propalaeoryx*.

TABLE 2

The Lower Dentition of *Canthumeryx*

	M.26682		M.26683		B.U.20111	
	Length	Width	Length	Width	Length	Width
D_3	16·3 mm	5·7 mm	—	—	—	—
D_4	22·2 mm	—	23·0 mm	11·1 mm	—	—
P_2	13·6 mm	5·3 mm	—	—	—	—
P_3	—	—	18·7 mm	8·6 mm	—	—
P_4	15·8 mm	7·5 mm	19·0 mm	9·8 mm	—	—
M_1	19·5 mm	11·0 mm	20·1 mm	14·0 mm	—	—
M_2	20·3 mm	13·6 mm	—	—	—	—
M_3	29·2 mm	13·3 mm	—	—	31·2 mm	13·7 mm

Palaeomeryx sp.

The presence of a species of the genus *Palaeomeryx* in the Gebel Zelten fauna is indicated by two fragmentary molars; M.26691 and B.U.20112. The specimens are both third molars of which the former is the more complete.

The metaconid is broken off but its postero-labial region indicates that it was joined to the protoconid and entoconid. The entoconid is transversely compressed and its posterior region is shortened, thus the posterior fossette opens lingually in contrast to *Canthumeryx*. The protoconid is crescentic and very stout, a '*Palaeomeryx* fold' may have been present but the posterior face of the protoconid is very heavily worn. The anterior end of the hypoconid is produced anteriorly and its posterior end which joins the entostylid is much longer than in *Canthumeryx*. The hypoconulid is stout and curves around the posterior end of the tooth, joining the entostylid and enclosing a posterior enamel island in contrast to *Canthumeryx* in which the posterior enamel island would not be formed in this position. A strong ectostylid is present in the median valley and a feeble stylid is present in the posterior valley of B.U.20112.

These specimens are distinguished from *Canthumeryx* by details of their dental anatomy and also by their smaller size; they resemble *Prolibytherium* closely in size but are more brachyodont and differ in anatomical details from this genus.

TABLE 3

The Lower Molars of *Palaeo*meryx sp

	M.26691	B.U.20112	K.R.442.51
M_3			
Length	24·2 mm	—	28·1 mm
Width of anterior lobe	11·5 mm	—	12·5 mm
Width of posterior lobe	11·0 mm	11·0 mm	13·0 mm
Width of accessory lobe	6·6 mm	6·7 mm	6·7 mm

Palaeomerycidae Indet.

A single pair of ossicones M.26690 (pl. 1, fig. 6), cannot be definitely assigned to any group of the Giraffoidea. These ossicones diverge at an angle of 40° and slope posteriorly at an angle of about 50° from the vertical. The bone surface has many fine vertical striations which fade out well above the base and it is unlikely that a horny sheath could have been present. The ossicones were very centrally positioned on the cranium and the region between them curves smoothly with no sign of a median suture. The small area of cranium that is preserved, indicates that the animal was slightly larger than *Prolibytherium*.

The cervid genus *Dicrocerus* has long pedicles which are comparable in form with this specimen but in *Dicrocerus* the pedicles were supra-orbitally situated and were less divergent. The ossicones of *Climacoceras* diverged at an angle of about 60° (MacInnes 1936), their internal structure is similar to ordinary bone with a core of vesicular structure; this agrees with M.26690. MacInnes (1936) also states that the shaft of *Climacoceras* was nearly straight throughout its length. The ossicones of *Climacoceras* may represent a condition derived from ossicones similar to M.26690.

Family **GIRAFFIDAE** Gray 1821

Diagnosis: Giraffoids in which the neck and limbs are usually lengthened. Ossicones small, consisting of a single tine. Degree of facial flexion small. Cheek teeth brachyodont; upper molars with strong mesostyle. Paracone and metacone having a diagonal orientation on the molar. Lower premolars exhibiting molarization. On the fourth lower premolar, the metaconid is strong and the hypoconid and entoconid are separated from the protoconid. '*Palaeomeryx* fold' usually absent.

Comments: This group previously included the Sivatheriidae which is here treated as a separate family of the Giraffoidea.

Subfamily **PALAEOTRAGINAE** Pilgrim 1911

Diagnosis: Primitive, medium sized giraffids, usually with one pair of supra-orbital, frontal ossicones. A second pair of ossicones may be present on the anterior extremities of the frontals. Skull usually elongate. Cheek teeth brachyodont. Limbs and neck slightly elongate. (After Colbert 1935a.)

Genus ***ZARAFA*** nov.

Diagnosis: A very primitive palaeotragine with flattened, laterally expanded frontals and frontal sinuses in the supraorbital region. Supraorbital ossicones present. Paired lacrymal foramina present on the anterior edge of the orbit. Basicranial and basipalatal planes almost parallel. Maxilla very shallow. Cheek teeth primitive and very brachyodont. A strong accessory crest present on the posterior region of the metaconule.

Zarafa zelteni sp. nov.

Diagnosis: As for genus.

Derivation of name: The generic name is from the Arabic for 'giraffe'. The trivial name is from Gebel Zelten, the area from which the type specimen was collected.

Holotype: An almost complete but edentulous skull (M.26670). The premaxilla and anterior region of the maxilla are missing and only the proximal region of the nasals is preserved. The lingual wall of the third molar is the only dental fragment preserved.

Locality: The material is all collected from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

Material:

M.26670	Holotype. An almost complete skull of an adult individual.
M.26671	A right maxillary fragment with P^4 to M^3. The dentition exhibits medium wear.
M.26672	A left maxillary fragment with D^2 to D^4. The first two permanent molars are dissected out.
M.26673	A cranial fragment consisting of the supra-occipital and parietal region.
M.26674	A cranial fragment with the frontal-parietal suture and the anterior part of the frontals preserved.
M.26675	A fragment of right mandible with M_3 showing light wear. The ascending ramus and condyle are preserved, though badly shattered.
M.26676	A heavily worn M_3.
M.26677	A lightly worn M_2.

Skull. The skull was found enclosed in a large sandstone nodule from which it was removed by the standard acetic acid preparation method. The postorbital region is in an excellent state of preservation but much of the preorbital region is missing. Slight crushing has occurred in the preorbital region. The specimen is from a mature individual but the acid preparation has opened and defined the sutures; these are not visible in areas prepared by hand.

Maxilla. It is likely that the maxilla was very shallow and probably resembled that of the juvenile giraffe. The postero-lateral region of the maxilla is missing but its shape is indicated as an internal cast (pl. 2). The facial tuberosity lies above M^2. The palatine process of the maxilla is badly broken and interpretation of the surface features is difficult. The surface is shallowly convex, its posterior edge extends to the maxillary tuberosity and into the orbit where it contributes to the lacrymal bulla. The anterior palatine foramen lies on the palatine-maxillary suture opposite the anterior end of the M^2; more posteriorly than in *Okapia* but similar to *Giraffa*. The anterior part of the bone is missing from the level of the anterior edge of P^2. The maxilla extends behind the third molar, forming a large maxillary tuberosity which is badly broken in the specimen.

Nasal. A small part of the nasal is preserved on the antero-dorsal edge of the prelacrymal vacuity. The bone is very flattened in the same plane as the frontal, as in *Palaeotragus microdon*.

Lacrymal. The large lacrymal forms the posterior edge of the prelacrymal vacuity and extends into the orbit. The antero-lateral face of the bone is concave in contrast to *Okapia* in which it is plane or *Giraffa* in which it is convex. The concavity in *Zarafa* results from the lateral expansion of the frontal bones. The lacrymal is expanded dorsally between the orbit and the prelacrymal vacuity. This dorsal expansion is more marked than in the other giraffids and may be due to the expansion of the frontals but a large lacrymal is also found in *Dremotherium*. A small lacrymal tubercle stands on the antero-dorsal edge of the orbit as in *Okapia* and paired lacrymal foramina are present behind the edge of the orbit. The maxillary foramen lies posterior to the lacrymal tubercle in the same position as in *Okapia*. The lacrymal bulla is badly broken posteriorly.

Jugal. The jugal forms the ventral and postero-ventral edges of the orbit and contributes about half of the postorbital bar; as in *Okapia* a strong ridge forms the ventral edge of the orbit. The lateral face of the jugal is concave and the ventro-lateral region of the bone is badly eroded. The facial region is large and elongate resembling the cervids rather than *Okapia*.

Palatine. Two parallel depressions run antero-posteriorly along the palatine. The bone is badly eroded posteriorly but it is preserved as a vertical plate in the pterygo-palatine fossa which is shallower but otherwise similar to that of *Okapia*.

Frontal. The orbital region of the frontal is concave with the orbital opening of the supraorbital canal lying in the most dorsal part. The ethmoid foramen lies ventro-medial to the supraorbital canal. The frontal-parietal suture runs dorsally from the alisphenoid to the top of the skull and medially across the dorsal face to the median suture (pl. 3). The temporal region of the frontal is very small its concave ventro-lateral face resulting from the great expansion of the posterior supraorbital crest. A strong postorbital ridge runs transversely between the supraorbital process of the frontal and the squamosal bone. The frontal forms the dorsal edge of the preorbital vacuity and dorso-lateral to this the bone thickens forming a high supraorbital crest. As in *Okapia* the supraorbital foramen is directly above the orbital opening of the supraorbital canal; a shallow concavity lies anterior to the foramen but there is no supraorbital groove in *Zarafa*. Lateral to the foramen the bone rises sharply to a peak and a process has been broken off revealing an extensive supraorbital frontal sinus which indicates the presence of a supraorbital ossicone. Ossicones are found in a similar position in *Palaeotragus microdon* and *Samotherium sinense* (Bohlin 1926) and this is probably the primitive position of ossicones in the Giraffidae. Postero-medial to this region is a strong lateral ridge which continues on the parietal.

Parietal. The temporal face of the parietal is dorso-laterally inclined with a convex anterior region and a concave posterior region. The parietal crest crosses the dorsal part of the temporal region and probably continued as far as the edge of the nuchal crest but the posterior region is missing. The dorsal face of the parietal is shallowly concave with raised lateral and medial ridges.

Occipital. The mastoid foramen lies on the postero-lateral face of the supraoccipital region and the occipital forms its ventro-medial wall (pl. 4, fig. 1). The shape of the nuchal crest was probably similar to that of *Okapia* but the supraoccipital region is broken dorsally (pl. 4, fig. 1) and most of the nuchal crest is missing. The occipital condyles and foramen magnum are large in *Zarafa* and dorso-medial to the edge of the condyle the bone surface is concave but it is produced as a large swelling over the foramen magnum, a similar swelling is present in *Palaeotragus microdon* but is less pronounced in *Okapia* and absent in *Giraffa* and *Prolibytherium.* Dorsal to the swelling the bone is excavated as insertion for the semispinalis capitis muscle; these excavations are shallower than in *Okapia.* A weak median occipital crest stands between the excavations but the external occipital protuberance is not preserved.

The paroccipital process projects ventrally to the level of the ventral edge of the condyles (pl. 4, fig. 1) as in *Okapia.* The basioccipital region has a pair of anterior occipital swellings between which the bone surface is concave, a median keel begins at the anterior end of this concavity and continues on the basisphenoid (pl. 4, fig. 2). The lateral face of the basioccipital is concave, this concavity giving way anteriorly to the paired basilar tubercles. The occipital-basisphenoid suture is closed. In *Okapia* the anterior swellings of the occipital condyles are much stronger than in *Zarafa* and the median keel is lost; in contrast a median depression runs posteriorly from the basioccipital—basisphenoid suture. The basilar tubercles are stronger and more elongate in *Okapia* than in *Zarafa.* The tubercles of the basioccipital provide insertion for the rectus capitis ventralis muscle which acts to flex the head downwards.

Sphenoid. The posterior region of the orbitosphenoid is concave with the optic foramen lying at its posterior end. Behind the optic foramen is a large foramen at the base of the alisphenoid. This foramen results from the fusion of the foramen rotundum and the foramen lacerum anterius (Colbert 1933) and through it emerge cranial nerves III, IV, VI and part of V, it is here referred to as the foramen rotundum. Behind the foramen rotundum the pterygosphenoid is produced as a ventral process (pl. 2) with convex lateral and concave medial faces. The ridge runs posteriorly from the posterior edge of the pterygosphenoid and forms the medial wall of the formen ovale through which the mandibular branch of cranial nerve V emerges. The foramen ovale is elongate in *Zarafa* as in *Okapia* and *Giraffokeryx* but in contrast to the giraffines and sivatheriids in which the foramen is circular (Colbert 1935b). Postero-lateral to the foramen ovale a groove runs along the edge of the basisphenoid and dorsal to the auditory bulla as far as the eustachian canal and the foramen lacerum medius. The basisphenoid is transversely convex with a strong median keel fading out anteriorly. The basisphenoid of *Okapia* does not bear a median keel but is otherwise very similar to that of *Zarafa.*

Squamosal. In *Zarafa* the squamosal surface is concave lateral to the foramen ovale. The temporal condyle of the glenoid gives way laterally and posteriorly to a glenoid cavity. The post-glenoid process is a strong, high, transverse ridge extending further laterally than in *Okapia* or *Giraffa.* The anterior edge of the glenoid region is formed by a strong ridge which begins at the alisphenoid tuberosity and continues laterally as far as the zygomatic arch. The squamosal is convex dorsally and contributes about half of the temporal wall of the skull, it is also produced laterally as part of the zygomatic arch. Over the ear region the squamosal forms a strong lateral tuberosity which contributes the postero-dorsal third of the external auditory meatus. The anterior edge of the tuberosity is produced into the temporal crest which runs anteriorly as far as the post-glenoid process. The squamosals of *Zarafa* and *Okapia* are similar.

Ear Region. In *Zarafa* the external auditory meatus is very ventrally situated, it is a postero-laterally directed tube formed by the petrosal and squamosal bones. The antero-lateral face of the external auditory meatus is concave with a strong hyoid process lying lateral to the bulla.

The bulla has a relatively thick wall, it is almost spherical in shape and is larger than that of *Okapia*. A large bulla is a primitive feature of the giraffids (Colbert 1938). The inner ear was partly exposed on the left side of the specimen; it is more elongate than that of *Prolibytherium* but appears to be similar in the main features of its ventro-lateral face. The fossa tensor tympani is very deep as in *Prolibytherium*. The bone surface is swollen postero-ventrally and above the swelling is a shallow concavity which leads anteriorly to the hiatus falloppii. These are the only parts of the inner ear visible.

The temporal canal opens between the ear region and the paroccipital process. Lateral to this the petromastoid suture runs dorsally between the squamosal and occipital regions. The petromastoid forms the postero-lateral part of the nuchal crest and has a concave posterior face.

Mandible. Only the posterior part of the mandible is known in *Zarafa*. The mandibular foramen is very large (pl. 4, fig. 3) and is situated more anteriorly in *Zarafa* than in *Okapia*. A deep depression runs from the foramen towards the condyle and from the ventral edge of the mandibular foramen a shallow groove runs antero-ventrally, this groove accommodates the lingual nerve and below it the face of the mandible is concave as far as the angle which was probably weak. Ventro-medial to M_3 the surface of the mandible is swollen and convex. The condyle is expanded laterally and medially with a slightly curved articular surface as in *Okapia*. The lateral face of the mandible is slightly convex and in the region behind M_3 the bone surface rises medially, forming a sharp medial ridge.

The Skull as a whole. The dorsal view of the skull (pl. 3) is dominated by the laterally expanded frontals but the extent, to which the lateral expansion of the frontals has effected the individual bones of the facial region, is difficult to assess. It is likely that the ancestral giraffids possessed a lacrymal fossa similar to that of the cervids; this assumption is made more probable by the condition of *Prolibytherium* and the concavity in *Zarafa* may represent a stage in the reduction of the fossa, however it is more likely that the expansion of the anterior supraorbital crest formed the concavity of the lacrymal. The dorsal expansion of the lacrymal in *Zarafa* may also be a primitive feature as *Dremotherium* has a large lacrymal bone but the lateral expansion of the frontals has probably influenced the lacrymal causing it to expand dorsally. The facial region of *Zarafa* exhibits some features that are certainly primitive; the paired lacrymal foramina, elongate jugal bones, shallow maxilla and large maxillary tuberosity are all features found in the cervids and palaeomerycids but absent in adult giraffids.

The main parameters of the gross cranial anatomy in the giraffids were studied by Colbert (1938) who used seven features of the skull in an attempt to establish the primitive features of *Okapia*. Owing to the broken nature of the skull of *Zarafa* only four of Colbert's parameters can be used (table 5). The degree of facial flexion is given as the angle between the basipalatal and basicranial axes; this angle is similar in *Dremotherium, Okapia, Zarafa* and *Palaeotragus microdon* and in these genera it is less than in advanced giraffids. The degree of facial flexion is usually treated as a measure of the evolutionary stage reached by the genus under consideration and on this basis *Zarafa* is as primitive as *Dremotherium* or *Palaeotragus microdon*. The angle between the basipalatal axis and the line joining the anterior edge of the orbit to the anterior border of the M^1, indicates that the orbit of *Zarafa* is more anteriorly situated than in the other giraffids except *Okapia* in which the orbit is in a similar position to that of *Dremotherium*. An anteriorly situated orbit is usually regarded as a primitive feature. The nasals are flat in *Zarafa* and *Palaeotragus microdon* but in the other giraffids and in *Dremotherium* the nasals are more flexed relative to the skull roof and the basipalatal axis. The condition of the primitive giraffid skull is discussed below and it is postulated that a wide, flattened skull roof is probably primitive for the giraffids.

In general shape of the skull, position of the ossicones and features of the basi-

TABLE 4

Zarafa zelteni. Measurements of the skull and dentition

The Skull

	M.26670	M.26673
Height above M^3	88 mm	
Postorbital length. (From anterior edge of orbit to occipital condyle)	187 mm	
Maximum width of frontals	179 mm	
Maximum width across occipital region	103 mm	
Width of occipital condyles	57 mm	
Maximum height of occipital region	78 mm	77 mm

The Upper Dentition

	M.26671		M.26672	
	Length	Width	Length	Width
P^4	15 mm	20 mm	—	—
M^1	19 mm	—	21 mm	19 mm
M^2	22 mm	24 mm	23 mm	22 mm
M^3	22 mm	23 mm	—	—
D^2	—	—	17 mm	8 mm
D^3	—	—	18 mm	13 mm
D^4	—	—	18 mm	15 mm

The Lower Dentition

	M.26675		M.26676		M.26677	
	Length	Width	Length	Width	Length	Width
M_2					25 mm	17 mm
M_3	33 mm	17 mm	32 mm	15 mm		

(All dental measurements are maximum.)

TABLE 5

Gross cranial features of *Zarafa zelteni*
(Measurements for *Okapia*, *Palaeotragus microdon*, *Giraffa* and *Giraffokeryx*, after Colbert 1938)

	Dremotherium	*Zarafa*	*Okapia*	*P. microdon*	*Giraffa*	*Giraffokeryx*
Angle between basipalatal and basicranial axes	5°	2°	4°	6°	17°	13°
Angle between basipalatal axis and line joining the anterior edge of the orbit to the anterior border of M^1.	82°	75°	82°	69°	71°	52°
Angle between basipalatal axis and superior border of nasals	18°	10°	17°	10°	31°	13°
Ratio of height of maxilla to premolar-molar length (Pm—M length = 100.)	68	59	105	94	130	93

cranial region *Zarafa* resembles the genus *Palaeotragus* and in particular the species *P. microdon.*

Upper Dentition. The deciduous dentition of *Zarafa* forms a closed series it is therefore likely that the permanent cheek teeth also formed a closed series from P^2 to M^3. The molars are more brachyodont than those of *Palaeotragus*, resembling in degree of brachyodonty the molars of *Palaeomeryx.* The enamel is finely rugose and the molars are four rooted with the lingual roots fused.

M^1 is almost square with the posterior half of the tooth displaced labially relative to the anterior half. The parastyle is strong and its labial rib is stronger than that of *Palaeotragus.* The paracone has a strong labial rib, similar to that of *Palaeomeryx* and stronger than that of *Palaeotragus.* The posterior end of the paracone lies lingual to the mesostyle which is the most labial part of the tooth. The metacone of M^1 is the same height as the paracone, its selene has a diagonal orientation on the tooth (pl. 5, fig. 1) and owing to the reduction of the labial rib it is more smoothly curved than the paracone. A weak metastyle forms the postero-labial corner of the tooth. The protocone is stout with a weak labial swelling which lends slight angularity to its crescentic shape, the posterior extension of the protocone terminates in the median valley without meeting the anterior face of the metaconule (pl. 5, fig. 1). The metaconule is higher than the protocone, its anterior region curves labially between the paracone and the metacone and from the anterior face of this region a small crest is produced into the median valley. A conule in the anterior fossette joins this crest and also joins the protocone and metacone giving an 'h' shaped wear trace (pl. 6, fig. 1). The metaconule has a stronger labial swelling than the protocone and behind this the height of the cusp is rapidly reduced. A long narrow accessory crest is produced from the metaconule and runs antero-labially to meet the base of the metacone (pl. 5, fig. 1). M^1 has strong anterior and posterior cingula. The M^1 of M.26672 (pl. 5, fig. 1) has a strong entostyle in the median valley, this arises from the base of the metaconule and does not join the protocone. M.26671 (pl. 6, fig. 1) has strong cingula in the median valley region but an entostyle is not developed. M^2 and M^3 are similar in the main features of their anatomy to M^1.

P^4 is three rooted and brachyodont with finely rugose enamel and anterior and posterior cingula which do not join as a lingual cingulum (pl. 6, fig. 1). The parastyle has a strong labial rib (pl. 6, fig. 2) as in *Palaeomeryx* but in contrast to *Palaeotragus* in which the labial rib of P^4 is feeble. The strong labial rib of the paracone curves anteriorly and carries a deep groove on its anterior face. The paracone of the *Palaeomeryx* P^4 is similar to that of *Zarafa* but in *Palaeotragus* the labial rib is reduced and the cusp is more compressed transversely than in the other two genera. The metacone has a weak swelling posterior to the paracone rib in *Zarafa* whereas in *Palaeomeryx* the labial rib of the paracone is clearly fused to the metacone rib, a groove indicating the line of fusion and in *Palaeotragus* a single rib is present with no posterior swelling. The protocone of the P^4 is stout and more regularly crescentic than in the molars; the anterior region joins the parastyle at an early stage of wear. On the posterior region of the protocone a weak accessory crest joins the base of the metacone and anterior to this crest a weaker parallel crest runs into the fossette but does not join the base of the metacone (pl. 6, fig. 1). This region of the P^4 differs from both *Palaeomeryx* and *Palaeotragus* but this crest is probably an individual variation of *Zarafa*.

D^4 is molariform (pl. 5, fig. 1), the parastyle is stronger than in the permanent molars with a strong labial rib. The paracone is thicker transversely than in the molars and in the anterior fossette there are a number of small conules (pl. 5, fig. 1). The mesostyle is stronger than in the molars, remaining as an independent style until late in wear. The metacone has a weak labial rib and the metastyle is stronger than in M^1 or M^2. The metaconule of D^4 is similar to that of the molars, a strong fold is produced from its anterior region into the median valley producing a forked anterior wear trace as in the molars. A strong accessory crest is produced from the posterior region of the metaconule and runs antero-posteriorly in contrast to the molars in which it runs antero-labially. A small entostyle is produced from the antero-lingual face of the metaconule into the median valley as in the molars. A cingulum stretches over the antero-lingual region of the protocone and a small cingulum covers the postero-lingual corner of the tooth.

D^3 is triangular with a single anterior root and a posterior pair. The enamel is smooth except on the lingual faces of the paracone and metacone where it is rugose. The parastyle is strong, existing as a separate style until late in wear, it lies near the anterior end of the tooth and the wear trace of the paracone branches labially to meet it. The paracone has a very strong labial swelling with an anterior groove. The metacone and its anterior and posterior styles are similar to those of D^4 or the molars. The protocone is elongate, its anterior region joins the protostyle which forms the anterior end of the tooth. A small crest is produced into the fossette opposite the parastyle and opposite the paracone a stronger crest is produced (pl. 5, fig. 1). The posterior end of the protocone joins the lingual part of the metaconule and there is no median valley. The metaconule of D^3 is similar to that of D^4, it is crescentic and in the anterior region it is produced between the paracone and metacone (pl. 5, fig. 1). A strong crest is produced from the anterior region of the metaconule into the posterior fossette, this crest runs posteriorly across the base of the metacone terminating near the middle of the fossette. An accessory crest is produced from the posterior region of the metaconule, this also runs to the middle of the fossette but does not join the anterior crest. A lingual cingulum runs along the base of the protocone ending in the middle of the tooth and a short cingulum is produced at the postero-lingual corner.

D^2 is very heavily worn and few surface features are visible. The parastyle is strong as in D^3 and joins a weak protostyle anteriorly. The paracone is high and more anteriorly situated than in D^3, it has a strong labial swelling. The metacone is elongate with a weak labial swelling. The protocone is small and its anterior region joins the protostyle and the parastyle, behind this is a weak crest as in D^3. There are three fine accessory crests on the posterior region of the metaconule (pl. 5, fig. 1). D^2 has a weak lingual cingulum which runs around the base of the metaconule and the posterior region of the protocone. The anterior region of D^2 resembles that of D^3 but the posterior region does not show any molariform features.

Lower Dentition. The lower dentition of *Zarafa* is known from a single M_2 and two third molars. These teeth are identified as *Zarafa* on the basis of their size, giraffoid features, height and enamel features.

M_2 resembles *Canthumeryx* in height and is lower than *Palaeotragus rouenii*. The mesostylid is weaker than in *Canthumeryx* or *Palaeotragus* and the metaconid rib is weak (pl. 5, fig. 3). In *Palaeomeryx* and *Canthumeryx* this rib is strong but in *Palaeotragus* it consists of a slight swelling of the surface. The entoconid has a weaker lingual swelling than in *Canthumeryx* or *Palaeomeryx* and resembles *Palaeotragus*. The posterior region of the entoconid is shortened but expands as a crest at some distance above the crown (pl. 5, fig. 3); a similar expansion is present in *P. rouenii* (M.8367) but in *Canthumeryx* the posterior crest is very strong throughout its height. The posterior fossette opens lingually (pl. 5, fig. 2). The anterior fossette is very shallow and widens at its anterior end (pl. 5, fig. 2); a similar widening occurs in *Palaeotragus* but not in *Canthumeryx*. The anterior cingulum is weaker in *Zarafa* than in *Canthumeryx* and the posterior cingulum is very short and small (pl. 5, fig. 2). M_2 has no ectostylid.

The metaconid of M_3 (pl. 5, fig. 4) is similar to that of M_2 (pl. 5, fig. 2) and is more nearly parallel to the axis of the tooth than in *Palaeotragus* or *Canthumeryx*. The metaconid rib is weak as in M_2 and the metastylid is also weak. The entoconid is similar to that of M_2 but in its posterior region it expands backwards to join the strong entoconulid (pl. 5, figs. 4 and 5) thus closing the posterior fossette. The protoconid and anterior end of the hypoconid are similar to those of M_2 but the posterior end of the hypoconid is flattened.

The accessory column consists of a stout hypoconulid which curves around the posterior end of the tooth, its antero-labial end abuts on the posterior end of the hypoconid and its lingual end curves anteriorly and joins the entoconulid (pl. 5, fig. 5). A strong ectostylid is present in the median valley and a weaker stylid stands in the posterior valley.

The cheek teeth of *Zarafa* show resemblances to both *Palaeomeryx* and *Palaeotragus* so that in some respects *Zarafa* may be regarded as intermediate between these genera. The labial ribs of the paracone and parastyle are weaker than is usual in *Palaeomeryx* though slightly stronger than in *Palaeotragus*. The mesostyle is strong in *Zarafa* as in *Palaeomeryx* but the smoothly curved general shape of the metacone and reduction of the labial metacone rib are very similar to *Palaeotragus* and contrast with *Palaeomeryx*. The protocones are similar in *Zarafa* and *Palaeotragus* and lack the strong postero-lingual spur which is present in *Palaeomeryx*. The cingula are more reduced in *Zarafa* than in *Palaeomeryx* but less reduced than in *Palaeotragus*. The upper molars of *Zarafa* are more hypsodont than in *Palaeomeryx* but are still much lower than in *Palaeotragus*. On the P^4 of *Zarafa* the labial ribs of the paracone and parastyle are stronger than in *Palaeotragus* though weaker than in *Palaeomeryx*, with this exception the P^4 is very similar in all three genera though a lingual cingulum is sometimes present in *Palaeomeryx* only.

The lower molars of *Palaeomeryx* are low crowned and wider relative to their length than in *Zarafa*, *Canthumeryx* or *Palaeotragus*. The lingual faces of the lower molars carry weak ribs in *Zarafa* and *Palaeotragus* whereas in *Palaeomeryx* these ribs are much stronger. A very weak '*Palaeomeryx* fold' is present in M.26675, this fold rarely occurs in *Palaeotragus* but it is usual and often strong in *Palaeomeryx*. The lower molars are higher crowned in *Zarafa* than in *Palaeomeryx* though lower than in *Palaeotragus*.

The upper and lower cheek teeth of *Zarafa* show features in which they resemble *Palaeotragus* and as these features are more advanced than the primitive ruminant condition they are interpreted as indicative of true relationship between the genera.

Post-cranial material. The Gebel Zelten collection includes a considerable amount of post-cranial material but owing to the conditions of preservation none of this material was found in association with the cranial elements. Specimens may be assigned to one or other of the ruminant genera with varying degrees of confidence, highest in the case of *Zarafa* which is the largest ruminant found at Gebel Zelten. In cranial features *Zarafa* is sufficiently like the other palaeotragines for the assumption to be made that the post-cranial elements must also show affinities with this group.

MATERIAL: B.U.20115—An almost complete right femur. B.U.20116—A complete right tibia. B.U.20117—A complete right metatarsal. B.U.20118—A complete left calcaneum. B.U.20119—A right calcaneum. B.U.20120—A right astragalus. B.U.20121—A left astragalus. B.U.20122—A left astragalus. B.U.20123—A left scapular fragment. B.U.20124—The distal end of a left humerus. B.U.20125—A right olecranon region. B.U.20126—The proximal end of a left radius. B.U.20127—The distal end of a left radius. B.U.20128—A fragment of a right metacarpal. B.U.20129—An anterior phalange. B.U.20130—A posterior phalange. B.U.20143—An anterior phalange. B.U.20144—A posterior phalange. B.U.20145—A posterior phalange. B.U.20146—The proximal end of a left tibia. B.U.20147—An axis. B.U.20148—An axis. B.U.20149—A seventh cervical vertebra. B.U.20150—A thoracic vertebra, probably the eighth. B.U.20151—A fourth lumbar vertebra. B.U.20152—A sixth lumbar vertebra.

The pectoral girdle

Scapula. The glenoid is shallowly concave and almost elliptical with a deep glenoid notch lying postero-lateral to the coracoid process (text fig. 7c). The coracoid process is strongly developed and projects further from the body of the bone than the tuber scapulae. In *Okapia* and *Giraffa* the tuber scapulae is very strongly developed and has grown over the coracoid process whereas in *Zarafa* the tuber scapulae is weak, consisting of a swelling lateral to the coracoid process. The surface of the tuber scapulae is heavily sculptured as the origin for the biceps brachii muscle. The spine of the scapula is shifted anteriorly and the supraspinous region is very narrow as in *Okapia*. The base of the spine indicates that it rises smoothly and an acromion process was probably present as in *Palaeotragus* and in contrast to *Okapia* and *Giraffa* in which this process is entirely absent. The absence of the acromion process appears to be related to the development of the tuber scapulae as in *Equus*, *Camelus* and large species of *Bos* the acromion process may be lost, in which case the tuber scapulae is of a size comparable to that of *Giraffa*. A strong tuber scapulae presumably indicates a greater development of the biceps brachii muscle and similarly reduction or absence of the acromion process indicates a reduction in the importance of the acromial part of the deltoideus muscle. The infraspinatus region is wide with a thickened posterior edge resulting in the concavity of the infraspinous fossa, the posterior edge is also concave as in *Giraffa*. The subscapular fossa is concave distally but the subscapular face of the neck is slightly convex. The shape of the neck of the scapula indicates that the blade was as elongate as that of *Okapia*. The anterior shift of the spine is also similar to *Okapia*.

Humerus. The distal end of the humerus is known from a single badly shattered specimen. The coronoid fossa is shallow with a deeply pitted surface and lateral to this the bone is expanded as a very strong lateral epicondyle similar to *Okapia* and *Giraffa*. The lateral condyle is wide with a concave surface and the medial condyle is also wide. The olecranon fossa is very deep. The distal end of the humerus is similar to that of *Okapia* and *Giraffa*.

Radius. The lateral tuberosity of the radius is weaker than in *Okapia* or *Giraffa* and the medial tuberosity is concave. These tuberosities provide attachment for the ligaments of the elbow and the smaller size of the lateral tuberosity indicates a weaker ligament; this is possible in a small relatively light animal such as *Zarafa*. The distal end of the radius has the usual three articular facets. The scaphoid facet is relatively wide; a concavity at the anterior end of the facet acts as a stop preventing over extension; this concavity is about the same depth in *Okapia* and shallower in *Giraffa*. The lunar facet has deep anterior and posterior depressions which also act as stops. The cuneiform facet is more oblique than the other two facets and its postero-medial region consists of a vertical concavity. The dorsal face of the bone has two strong ridges as in *Okapia*. The shaft of the bone, although incompletely known, appears to have been more slender than in *Okapia*.

Ulna. The olecranon process of the ulna is the only region preserved. The semilunar notch is transversely narrow and the edges of the facet are rounded giving it a transversely convex shape which agrees closely with that of *Giraffa*. In *Okapia* the semilunar facet is transversely plane which greatly restricts the lateral mobility of the elbow. The semilunar region is produced disto-laterally as a strong process articulating partly with the lateral condyle of the humerus and partly with the posterior face of the radius; this facet is similarly developed in *Giraffa*. The olecranon process is short and transversely flattened with a concave medial face. The distal end is heavily sculptured for the insertion of the triceps muscle.

Metacarpal. The facets of the proximal end are similar to those of *Okapia* and on the postero-medial face of the proximal end the surface of the bone is heavily sculptured as in *Okapia* but there is no indication of metacarpal V. The presence of this metacarpal is variable in *Giraffa* (Fraser 1951) and may also have been variable in *Zarafa*. The shaft of the metacarpal is more slender than that of *Okapia;* its cross-section is flattened as is usual in the ruminants, with a deep channel on the posterior face to accommodate the flexor tendons. The distal head has the usual paired condyles converging slightly as in *Giraffa*. The keel of the condyle is very strong and in the posterior region it extends proximally as a strong ridge over the articular face and beyond this onto the body of the bone. The strength of this keel resembles the cervid condition. In both *Okapia* and *Giraffa* the condyle is expanded in the interdigital region which reduces the apparent strength of the keel. The distal head of the metacarpal is much wider than the shaft in *Zarafa*, *Giraffa* and the cervids but in *Okapia* it is only slightly wider as the shaft is thickened.

Phalanges. The phalanges are very slender. Their postero-proximal epicondyles are very short whereas in *Okapia* and *Giraffa* they are elongate, covering about one third of the posterior face of the phalange. The interdigital face has a weak tuberosity in the distal region to which the interdigital ligament attaches. The distal articular face consists of a central depression flanked by two expanded areas which extend over the end of the bone; this facet is slightly oblique which causes the second phalange and hooves to move towards each other when weight is placed on the foot.

Five phalanges are identified with *Zarafa*, these include two larger and three small ones. The difference in size between these groups is approximately the same as the size relationship between the anterior and posterior phalanges of *Okapia*; for this reason the larger are identified as anterior and the smaller as posterior. The smaller phalanges will not be described separately with the description of the pelvic limb.

The Pelvic Limb

Femur. The head of the femur is small relative to the length of the bone; its articular surface extends onto the neck and around the lower side of the head as in *Okapia.* The neck of the femur is long and the head is displaced further medially than in *Okapia* or *Giraffa.* In both *Okapia* and *Giraffa* certain tendencies towards a graviportal condition of the limbs are evident, these tendencies are most apparent in the rotation of the articulations into the line of the shaft. The greater displacement of the articulations or curvature of the shaft of the limb bones in *Zarafa* indicates a lighter animal. The trochanter minor is weak and is not displaced as far medially as it is in *Okapia* or *Giraffa*; as a result the trochanteric ridge appears stronger in *Zarafa* than in the extant giraffids.

The distal region of the femur is of the usual ruminant pattern. On its anterior face the medial ridge is high and expanded but is less swollen than that of *Okapia* or *Giraffa,* this indicates that the 'stifle joint' was less effective than in *Okapia* or *Giraffa* as expected in a smaller lighter animal (Shuttleworth 1943). The medial and lateral epicondyles are very strong but are less transversely expanded than those of *Okapia.* The shaft of the femur is slender and slightly curved anteriorly (posterior face concave) as in the medium sized cervids and in contrast to *Okapia* and *Giraffa* in which the shaft is straight and relatively stout. The supracondyloid fossa is more elongate than in *Okapia,* this is probably due to the generally narrower nature of the distal region in *Zarafa.*

The femur of *Zarafa* is much more slender than that of *Okapia* and both extremities are narrower. The curvature of the shaft indicates a lightly built animal and features such as the position of the trochanter minor are similar to the cervid condition.

Tibia. The proximal head of the tibia is narrow transversely as in the cervids and in contrast to *Okapia* or *Giraffa* in which the head is relatively wide. The cnemial crest is high and blends gradually into the shaft over the proximal quarter of its length; this crest is similar in the medium sized cervids but in *Okapia* it occupies the proximal third of the anterior face. The antero-proximal region of the cnemial crest forms a large triangular tuberosity bounded laterally by the sulcus muscularis and medially by a shallow depression through which the middle patellar ligament passes. A small tubercle is produced posterior to the spine, this is similar to that of *Okapia* and provides attachment for the posterior cruciate ligament.

The distal end of the tibia is much narrower in *Zarafa* than in *Okapia* and in general features it resembles the cervid tibia. The shaft is slightly curved posteriorly as in the cervids and in contrast to *Okapia* in which the shaft is straight. The tibia of *Zarafa* is relatively shorter than that of *Capreolus* but longer than that of *Okapia* or *Giraffa*. It is similar in its main features to the tibia of *Giraffa* which is more primitive than that of *Okapia*.

Calcaneum. The tuber calcis is very long and similar to *Capreolus* or *Palaeomeryx* whereas in *Palaeotragus* and *Samotherium* it is slightly shortened and in *Okapia* and *Giraffa* it is extremely shortened. The tuber calcis is more flattened than in *Okapia*. The posterior face of the sustentacular process is plane whereas in *Okapia* and *Samotherium* it is concave. The lateral face of the calcaneum bears an area of heavy sculpturing occupying most of the antero-proximal region, posterior to this is a small oval facet to which the lateral ligament of the ankle attaches. The fibular facet is of the usual primitive form with a raised convex posterior region and a concave anterior region as in *Palaeomeryx* and in contrast to *Okapia* in which this facet is specialized by the loss of the anterior region. The facet in *Zarafa* indicates that the fibula was probably similar to that of *Capreolus*. The sustentacular facet is wide and transversely convex, it does not show any reduction of the proximo-medial corner, such as is found in *Okapia* and *Giraffa* as a specialization facilitating greater flexion of the ankle. The calcaneum is generally more like that of the cervids than the extant giraffids, this is however partly due to the specialization of the ankle in *Okapia* and *Giraffa*.

Astragalus. This is more elongate than in *Okapia* or *Giraffa* and compares very closely in all its main features with the astragalus of *Palaeomeryx*.

Metatarsal. The proximal facets of the metatarsal are similar to those of *Okapia*. A deep notch lies on the lateral edge of the bone between the facets, this probably housed metatarsal V which appears to have been well developed in contrast with the extant giraffids in which it is represented as a thin ribbon of bone, entirely fused to the lateral face (Fraser 1951). A strong tubercle lies between and medial to the facets, this is metatarsal II and is stronger than in *Giraffa* or *Okapia*; it continues on the medial face as a wide ribbon of bone fused to the shaft and continuing much further distally than in *Giraffa*.

The shaft of the metatarsal is very long and slender in *Zarafa*, it has a deep cross-section as in *Giraffa*, *Samotherium* and *Palaeotragus*, this is narrower transversely than in *Okapia*. The two condyles of the distal extremity are similar to those of *Giraffa* but the ridges of the condyles are stronger as on the metacarpal. A deep channel runs down the anterior face of the bone, this channel is open for its whole length as in *Okapia*, *Giraffa* and the bovids whereas in the cervids the channel is roofed over in the distal region.

Vertebrae

Axis. The axis of *Zarafa* is smaller and more elongate than that of *Okapia*. The neural spine has a high posterior tubercle (text fig. 2a) from which it slopes downwards anteriorly and projects over the odontoid process as in *Okapia*. The odontoid process is similar to that of *Giraffa* and the anterior articular facet has a depression near to and around the base of the odontoid process as in *Giraffa* but in contrast to *Okapia* in which the facet blends into the odontoid process. The anterior articular facet slopes almost vertically as in *Giraffa*. The intervertebral foramen (text fig. 2a) is in the same position as that of *Okapia*, it has a deep postero-ventral channel which joins it to the anterior channel of the vertebrarterial canal. This canal begins near the middle of the bone and emerges on the posterior face, dorso-lateral to the articulation. The posterior articular process is less pronounced than in *Okapia*, its articular facet is almost circular and faces postero-ventrally. The transverse

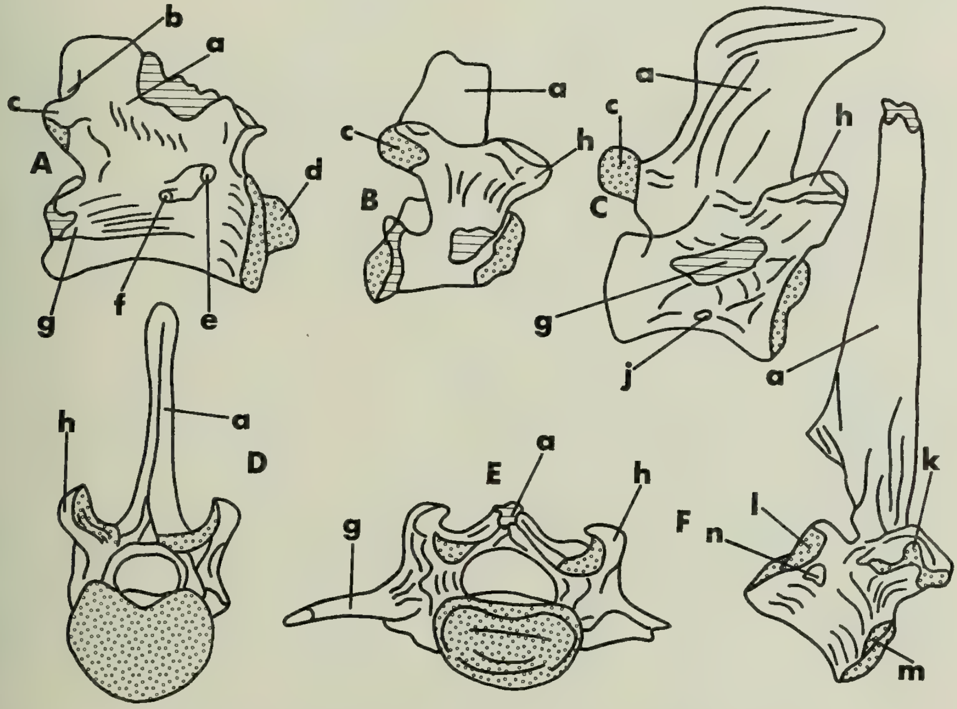

FIG. 2. The vertebrae of *Zarafa*. (Half natural size.). (A) Lateral view of the axis (B.U.20148). (B) Lateral view of the seventh cervical vertebra (B.U.20149). (C) Lateral view of the fourth lumbar vertebra (B.U.20151). (D) The anterior face of the fourth lumbar vertebra (B.U.20151). (E). Anterior face of the sixth lumbar vertebra (B.U.20152). (F) Lateral view of the eighth thoracic vertebra (B.U.20150). a: neural spine. b: posterior tubercle. c: posterior articular process. d: odontoid process. e: intervertebral foramen. f: vertebrarterial canal. g: transverse process. h: anterior process. j: nutrient foramen. k: tubercular facet. l: posterior facet for the head of the rib. m: anterior facet for the head of the rib. n: tuberosity.

process is more slender than that of *Okapia* and is more dorsally situated; lying at the same level as the top of the centrum (text-fig. 2a). The posterior articular face of the centrum is concave as in *Okapia*; and in *Zarafa* it is more nearly vertical than in *Okapia.*

Cervical vertebra. The seventh cervical vertebra (text fig. 2b) is similar to that of *Okapia* with no signs of the specialization found in *Giraffa* (Lankester 1908). The centrum is thicker than in *Okapia* and both anterior and posterior articulating faces of the centrum are more nearly vertical in *Zarafa* than in *Okapia;* in this feature the vertebra is similar to that of *Giraffa.* The anterior articulating processes are more widely divergent than in *Okapia* but the articulating facets are orientated at the same angle in both genera. The posterior articular processes are lateral only with no indication of the medial articulation such as occurs in *Okapia* (Lankester 1910). The facets are elongate which indicates that there was considerable freedom of movement of the lower neck region.

Thoracic region. A single thoracic vertebra (B.U.20150) agrees closely with the eighth thoracic vertebra of *Okapia.* The anterior face of the centrum is shallowly convex and the facet extends ventrally as it does in *Okapia.* The facet for the head of the rib (text fig. 2f) is more closely blended with the centrum face than in *Okapia.* The ventral ridge is strong with a tubercle in the postero-dorsal corner of the concave lateral face (text fig. 2f), this is equally well developed in *Okapia.* The posterior face of the centrum is concave with the facets for articulation with the rib situated high up at the dorso-lateral corners of the face (text fig. 2f). The transverse process is well developed with a tubercular facet running antero-dorsally from its ventro-lateral region. The mamillary process is only weakly developed and is more laterally situated than in *Okapia.* Both anterior and posterior articular processes are deformed as only the left side is developed in each case and the facets on this side have undergone compensatory size increases. The neutral spine is very slender and its posterior region is only slightly thickened; the spine was probably higher than in *Okapia* and more posteriorly inclined.

Lumbar vertebrae. The fourth lumbar vertebra (B.U.20151) is more elongate than in *Okapia* or *Giraffa* with a strong ventral ridge and ventro-lateral concavities as in *Okapia.* A large nutrient foramen lies lateral to the ventral ridge, just anterior to the middle of the centrum (text fig. 2c); in *Okapia* and *Giraffa* many small foramina are found in this region. The anterior face of the centrum is shaped as shown (text fig. 2d) and the posterior face is expanded slightly transversely as in the other giraffids. The anterior articular process is strong and high with a medially concave articular facet as is usual in the lumbar region of the ruminants. The posterior articular process is short and resembles *Giraffa* as it faces ventro-laterally, rather than laterally as it does in *Okapia.* The posterior articular process is not produced as far posteriorly as it is in *Okapia.* The neural spine is stout and high; it is expanded anteriorly in the distal region which is also thickened and has an excavated surface for the insertion of the longissimus dorsi muscle.

The sixth lumbar vertebra (B.U.20152) is free with a transversely expanded centrum (text fig. 2e) bearing a strong ventral ridge in the anterior region only. The anterior articular process has an elongate articular facet directed postero-ventrally as in *Giraffa* and not ventrally as in *Okapia* which indicates a greater freedom of movement at this joint in *Zarafa* and *Giraffa* than in *Okapia*. The transverse process (text fig. 2e) is slender and slopes slightly ventrally as in *Giraffa*. The facet of the posterior articular process is elongated antero-posteriorly but is not as long as that of *Giraffa*. The neural spine is more anteriorly situated in *Zarafa* than in *Giraffa* and the posterior part of the centrum is slightly elongated.

Functional Interpretations. The forelimb and vertebral column of *Zarafa* are poorly known and it is not possible to make any meaningful functional interpretations of these regions. Fortunately the hind-limb is almost completely known and it has been used to assess the degree of cursorial adaptation attained.

The main recent study of functional features of the limbs of mammals is that of Smith and Savage (1956) who in their section on the hind limb deal only with the muscles originating on the pelvis. In *Zarafa* the pelvis is not known and therefore this group of muscles cannot be studied but the mechanical advantage of the biceps femoris and semi-tendinous muscles, which insert on the cnemial crest, can be estimated using the formula:

$$\begin{array}{l}\text{Mechanical advantage of biceps}\\ \text{femoris and semitendinous muscles}\end{array} = \frac{\text{Height of cnemial crest}}{\text{Total length of lower leg}}$$

In this equation it is assumed that the femur and pelvis are rigid which they are not; but the accuracy of the figures obtained is sufficiently high as the formula is used for comparative purposes rather than to obtain absolute measurements. The height of the cnemial crest of the tibia is measured from the posterior face of the tibial spine and the length of the lower leg is measured vertically from the knee to the ground.

If the mechanical advantage of the locomotory muscles is high then a slow powerful action is indicated as found in graviportal animals. A low mechanical advantage of the locomotory muscles indicates a weak but rapid action and is characteristic of cursorial animals, thus the mechanical advantage of a group of muscles may be used to measure the degree of cursorial adaptation attained. Table 7 indicates that *Giraffa* has a lower mechanical advantage for the biceps femoris than the other genera and *Giraffa* is more cursorially adapted than these genera. In degree of cursorial adaptation, as measured using the muscles inserting on the cnemial crest *Zarafa* lies between *Okapia* and *Capreolus*.

The mechanical advantage of the gastrocnemius muscle which inserts on the end of the tuber calcis can be estimated using the formula:

$$\begin{array}{l}\text{Mechanical advantage of}\\ \text{gastrocnemius muscle}\end{array} = \frac{\text{Length of tuber calcis}}{\text{Length of ankle and pes}}$$

As may be expected *Giraffa* again exhibits considerably greater cursorial adaptation than the other genera and *Zarafa* again lies between *Okapia* and *Capreolus* (table 7).

The osteological features of *Zarafa* indicate a lightly built animal and this is borne out by features of the limbs which taper rapidly and are very slender, thus the low degree of cursorial adaptation, as measured from the mechanical advantages of the muscles, must be interpreted as a primitive feature of *Zarafa*.

TABLE 6

Measurements of *Zarafa zelteni* post-cranial elements

Vertebrae

	B.U.20147	B.U.20148	B.U.20149	B.U.20150	B.U.20151	B.U.20152
Length of centrum	69 mm	65 mm	32 mm	34 mm	47 mm	37 mm
Total height of vertebra	63 mm	68 mm	72 mm	131 mm	91 mm	47 mm
Depth of centrum	20 mm	19 mm	23 mm	24 mm	23 mm	21 mm
Width of anterior end of centrum	52 mm	49 mm	19 mm	28 mm	35 mm	37 mm
Width of posterior end of centrum	35 mm	34 mm	34 mm	36 mm	39 mm	48 mm

Scapula

	B.U.20123
Width of neck of scapula (Min.)	36 mm
Depth of neck of scapula (Min.)	19 mm
Width of glenoid (Ant-post)	47 mm
Depth of glenoid (Transverse)	39 mm

Humerus

	B.U.20124
Distal end	
Width across epicondyles	59 mm
Antero-posterior depth of distal articular surface	27 mm

Radius

	B.U.20126	B.U.20127
Width of proximal articular surface	49 mm	
Depth of proximal articular surface:		
Minimum	29 mm	
Maximum	18 mm	
Width of distal articular surface		44 mm
Depth of distal articular surface		29 mm

Metacarpal

	B.U.20128
Length	317 mm
Width of distal end	46 mm
Depth of distal end	25 mm

Phalanges

	B.U.20129	B.U.20143	B.U.20144	B.U.20145	B.U.20130
Length	70 mm	68 mm	63 mm	62 mm	58 mm
Width of proximal end	21 mm	21 mm	20 mm	19 mm	20 mm
Depth of proximal end	23 mm	25 mm	23 mm	24 mm	23 mm
Width of distal end	16 mm	18 mm	16 mm	16 mm	17 mm
Depth of distal end	14 mm	15 mm	12 mm	13 mm	12 mm

Femur

	B.U.20115
Total length (Maximum)	341 mm
Width of proximal end	84 mm
Depth of articular head	36 mm
Width of distal end	66 mm
Depth of distal articular head:	
Maximum	83 mm
Minimum	58 mm

Table 6 (*cont.*)

Tibia

	B.U.20116	B.U.20146
Length	349 mm	—
Width of proximal end	68 mm	69 mm
Depth of proximal end	76 mm	72 mm
Width of distal end	46 mm	—
Depth of distal end	35 mm	—

Calcaneum

	B.U.20118	B.U.20119
Total length	108 mm	115 mm
Length of tuber calcis	74 mm	76 mm
Width across sustentaculum	34 mm	32 mm
Depth of tuber calcis	28 mm	27 mm
Maximum depth of bone	41 mm	42 mm

Astragalus

	B.U.20120	B.U.20121	B.U.20122
Maximum length	49 mm	41 mm	53 mm
Minimum length	40 mm	40 mm	41 mm
Width proximally	29 mm	30 mm	32 mm
Width distally	29 mm	29 mm	30 mm
Maximum depth	23 mm	23 mm	25 mm

Metatarsal

	B.U.20117
Length	349 mm
Width of proximal end	39 mm
Depth of proximal end	41 mm
Width of distal end	42 mm
Depth of distal end	29 mm

Table 7

Measurements used for functional interpretation of the *Zarafa* hind limb

	Giraffa	*Okapia*	*Zraafa*	*Capreolus*
Height of cnemial crest of tibia	10·5 mm	5·7 mm	6·5 mm	3·5 mm
Total length of lower leg	179·0 mm	87·5 mm	87·0 mm	45·5 mm
Length of tuber calcis	15·9 mm	8·6 mm	8·7 mm	5·0 mm
Length of ankle and pes	110·0 mm	51·0 mm	50·0 mm	26·0 mm
Mechanical advantage of biceps femoris muscle	0·059	0·065	0·075	0·077
Mechanical advantage of gastrocnemius muscle	0·163	0·166	0·174	0·192

Family **SIVATHERIIDAE** nov.

Diagnosis: Large giraffoids with strongly expanded frontal bones and pneumatized skull roof. On the frontal and parietal bones a pair of large, flattened, variably branched ossicones is produced. A great increase in overall body size occurs in advanced genera but elongation of the limbs and neck does not occur.

Remarks: This group has previously been treated as a subfamily of the Giraffidae but the presence of *Prolibytherium* and *Zarafa* in deposits of early Miocene age indicates a division which extends back into the Oligocene. A more natural grouping results if the Palaeotraginae and Giraffinae are grouped together in the Giraffidae and the Sivatheres are placed in a separate family the Sivatheriidae.

Genus *PROLIBYTHERIUM* Arambourg 1961

Diagnosis: A primitive sivatheriid of small size. The cranium is narrow and exhibits very little facial flexion. The frontals support large, aliform ossicones which extend anteriorly in the supraorbital region and posteriorly over the parietal and occipital region. The occipital condyles are large with very thickened bone. A lacrymal fossa and paired lacrymal foramina are present.

Prolibytherium magnieri Arambourg 1961

Diagnosis: As for genus.

Holotype: A cranium with badly shattered ossicones, described by Arambourg (1961a).

Locality and horizon: The material is all collected from the Lower Miocene (Burdigalian) deposits of Gebel Zelten, Libya.

Remarks: Specimens in l'Institut de Paléontologie, Paris, include dentitions of *Prolibytherium* but these were not found with the type material and were not described by Arambourg.

Material: Specimens in l'Institut de Paléontologie are defined by capital letters.

M.21901	An almost complete skull; the ossicones, cranium and left maxilla are complete. The upper dentition is heavily worn and lacks P^3.
M.21899	A right mandible with heavily worn dentition.
M.26678	An endocranial cast that was dissected out of a skull.
M.26679	A fragment of cranium, with ossicones and bearing the only large lacrymal fragment.
M.26680	An edentulous mandible which has a complete diastema.
M.26681	An isolated lower third molar, lightly worn.
P.M. A.	An almost complete mandible with P_2 to M_3 exhibiting slight wear.
P.M. B.	A mandibular fragment with almost unworn M_1 to M_3.
P.M. C.	A mandibular fragment with heavily worn M_1. The P_4 was displaced to the side during life and is thus virtually unworn.
P.M. D.	A mandibular fragment with heavily worn M_1 to M_3.
P.M. E.	P_3 and P_4, both lightly worn.
P.M. F.	A badly shattered M^3. The paracone and antero-labial region is missing but the metacone is complete.
B.U.20175	A right mandible with heavily worn P_3 to M_3.
B.U.20176	A cranium with the external auditory meatus preserved.

THE SKULL AND DENTITION

The Skull. The skull roof is entirely covered by large ossicones (pl. 7) which are completely fused to the frontal and parietal bones without any visible suture. The facial region is incompletely known as the premaxillary and nasal bones are not preserved and the jugal is known from a single small fragment. A complete lacrymal has not been discovered but several large fragments of the lacrymal are known. With these exceptions the cranial elements are almost completely known from well preserved specimens.

Maxilla. The maxilla of M.21901 is broken near the postero-labial alveolus of M^3, the break continuing antero-dorsally along the maxillary jugal suture (text fig. 3a). The maxilla is complete dorsally as far as the maxillary-nasal suture and anteriorly it is broken along what is probably the maxillary-premaxillary suture (pl. 8). The lateral surface of the maxilla is convex with a feeble facial crest which joins the weak facial tuberosity at its posterior end. The infraorbital foramen is slightly larger than the lingual alveolus of P^3; it is deeply inset below the curve of the maxilla above P^2 as in *Sivatherium* and *Capreolus* (text fig. 3b). In *Okapia* and *Giraffa* the infraorbital foramen is more anteriorly situated than in *Prolibytherium*; this difference may be due to the expansion and increased height of the maxilla in the extant giraffids. The molars and P^4 have a diagonal orientation relative to the main contours of the maxilla which results in strong juga alveolaria on the surface of the maxilla (pl. 8). Above the facial tuberosity the surface of the maxilla is deeply concave indicating the presence of a lacrymal fossa (pl. 8), this region agrees closely with that of *Capreolus* and differs from *Okapia* and *Giraffa*. Above this region the maxilla forms the antero-ventral border of the preorbital vacuity (text fig. 3a), this edge is similar to that of *Capreolus* (text fig. 3b).

The palatine process of the maxilla is shallowly concave with the median suture raised above the bone surface. The anterior palatine foramen is level with the antero-lingual corner of M^2 and the palatine groove runs anteriorly from it (pl. 9). Behind M^3 is a large maxillary tuberosity as in *Palaeomeryx* and *Zarafa*.

The maxilla of *Prolibytherium* is very shallow in the region under the orbit, as in *Zarafa*. The maxillae of *Prolibytherium* and *Capreolus* agree closely in shape (text fig. 3b); this agreement is less close in the posterior region where the maxilla is reduced in *Capreolus* and the jugal is expanded ventrally.

Lacrymal. The orbital face of the lacrymal is concave and the border of the orbit is sharp. Paired lacrymal foramina are present, the dorsal foramen lies behind the lacrymal tubercle and in *Prolibytherium* both foramina lie behind the edge of the orbit whereas in *Capreolus* they are situated on the edge of the orbit. The anterior face of the lacrymal is very concave and the bone is thin ventrally. Although the ventral part of the lacrymal is not known, the concavity of the dorsal region and the reduction in thickness of the bone agree with the concavity of the dorsal part of the maxilla and indicate the presence of a deep lacrymal fossa. A lacrymal fossa is absent from all giraffids and the other sivatheriids but is present in cervids and in some bovids. In the cervids this fossa houses the facial gland which produces a secretion used in territorial marking. The establishment and maintenance of a territory involves a certain amount of intraspecific combat and the occurrence of this in *Prolibytherium* is also indicated by the large ossicones. The presence of a lacrymal fossa in *Prolibytherium* the cervids and *Dremotherium* could result from parallel development but in this instance it is more likely that its presence is a primitive feature.

Jugal. A fragment of the jugal is preserved attached to the maxilla (text fig. 3a). The dorsal edge of this fragment runs postero-ventrally and is probably the suture with the lacrymal. The flattened antero-dorsal face of the jugal is continuous with the lacrymal fossa.

Palatine. The palatine is transversely concave and the depth of this concavity increases posteriorly (pl. 9). The anterior palatine foramen opens on the anterior suture. The median suture is slightly raised as on the maxilla and the posterior end of the palatine is deeply indented forming the edge of the pterygo-palatine fossa (pl. 9); here the bone is vertical with a lateral face which is continuous with the maxillary tuberosity. The lateral face of the palatine is penetrated by the posterior palatine foramen which is similarly situated in *Capreolus* but is higher in *Okapia.*

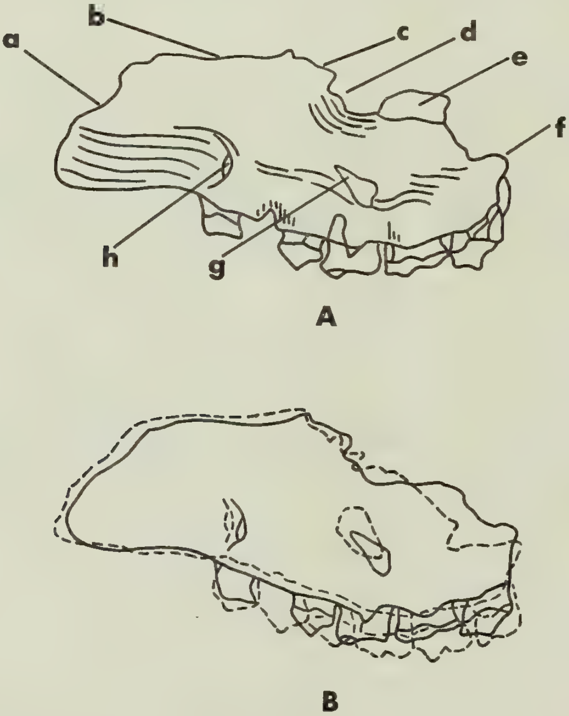

Fig. 3. The maxilla of *Prolibytherium* (B.M.21901). (Half natural size). (A) Lateral view of the maxilla. a: maxillary-premaxillary suture. b: maxillary-nasal suture. c: border of preorbital vacuity. d: lacrymal fossa. e: fragment of jugal bone. f: maxillary-jugal suture. g: facial tuberosity. h: infraorbital foramen. (B) Comparative outlines of the maxilla in *Prolibytherium* and *Capreolus*. *Prolibytherium* ——————: *Capreolus* ----------------

Frontal. The orbital region of the frontal is concave and the orbital opening of the supraorbital canal is in the dorsal region of this concavity; probably as a result of the thickening of the bone, this opening is situated more medially than in *Okapia* or *Giraffa.* From its orbital opening the supraorbital canal runs dorso-medially for a short distance before turning sharply anteriorly, it continues in this direction as far as the dorsal face, thus opening much more anteriorly than is usual in the ruminants. The medial edge of the supraorbital process forms a strong ridge which continues medially as far as the alisphenoid tuberosity. The temporal region of the frontal is convex dorso-ventrally and blends into the ossicone in its dorsal region. The supraorbital foramen is anterior to the highest part of the orbit and the deep supraorbital groove runs anteriorly from the foramen to the lateral end of the frontal-nasal suture (text fig. 4). The supraorbital crest is formed by the thickening of the frontal along the edge of the orbit. Behind the supraorbital foramen the bone forms a triangular depression bounded antero-laterally by the supraorbital crest and medially by the median suture which is raised into a crest running posteriorly as far as the frontal eminence (text fig. 4).

Parietal. The lateral face of the parietal is convex and the dorsal region fuses with the ossicone. In front of the occipito-parietal suture the dorso-lateral face of the bone is concave with a strong parietal crest which blends into the ossicone anteriorly. The opening of the large temporal canal is visible on the broken edge of the bone (pl. 7).

Ossicones. The ossicones fuse completely with the expanded frontal and parietal bones, they are large and aliform and have been arbitrarily divided into anterior and posterior palmations for the purposes of description (text fig. 4). From the frontal eminence a strong crest runs antero-laterally forming the posterior edge of the triangular supraorbital concavity of the frontal (text fig. 4); this crest continues laterally as the leading edge of the anterior palmation. Another crest runs postero-laterally from the frontal eminence and forms the thick posterior edge of the posterior palmation. Lateral to these crests the ossicones become much thinner with concave dorso-lateral faces.

The dorsal and ventral surfaces of the ossicone bear a large number of fine, radiating grooves (pl. 7). Immediately dorsal to the supraorbital process is a small foramen on the leading edge of the anterior palmation, a deep groove originates from this foramen and runs postero-laterally across the lateral concavity of the ossicone, giving off many smaller branches over the surface.

The ventral surface of the ossicone is convex antero-posteriorly and shallowly concave transversely. A large groove begins postero-lateral to the supraorbital process and runs postero-laterally nearly to the edge of the ossicone where it forks, one branch follows the lateral edge of the anterior palmation and the other follows the edge of the posterior palmation. Above the glenoid cavity a large foramen, at the base of the ossicone, gives rise to a deep groove which divides into many fine grooves radiating over the lateral surface of the ossicone. A medial foramen is situated above the occipital region, at the base of the ossicone, lateral to this is a stout column beyond which is a larger lateral foramen (pl. 10, fig. 2) many fine grooves radiate from this foramen.

Occipital. The dorsal surface of the supraoccipital region is convex as far as the nuchal crest. In the palaeotragines the supraoccipital region is reflected over the condyles but in *Prolibytherium* it is vertical or slopes slightly anteriorly as in *Capreolus*. The mastoid process forms the lateral wings of the nuchal crest and the supraoccipital forms the dorsal part of the crest (pl. 10, fig. 2). The medial edge of the mastoid foramen is formed by the occipital bone. On the posterodorsal face of the supraoccipital region are paired depressions providing insertion for the semispinalis capitis muscles—the chief extensors of the head and neck. The external occipital protuberance lies medio-ventral to these pits (pl. 10, fig. 2), its surface is deeply sculptured (pl. 10, fig. 2) for attachment of the nuchal ligament. The ventral part of the external occipital protuberance is produced ventrally as a strong median crest. The occipital condyles have sharp keels on their lateral faces (pl. 10, fig. 1). The condyles are set very close to the skull; they are relatively large and the bone is

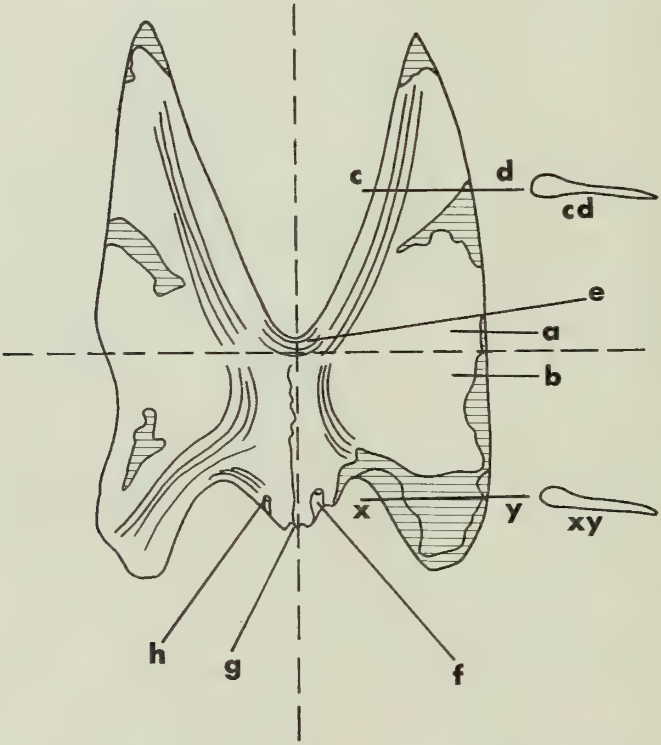

FIG. 4. Dorsal view of the ossicones of *Prolibytherium* (B.M.21901) (One sixth natural size.). a: posterior palmation. b: anterior palmation. c–d: cross-section of the ossicone. e: position of frontal eminence. f: supraorbital groove. g: fronto-nasal suture. h: dorsal opening of supraorbital canal. x-y: cross-section of the ossicone.

greatly thickened. The foramen magnum is small relative to *Okapia* or *Giraffa* and the incisura intercondyloidea, which is strong is the giraffids, is reduced to a small notch on the ventral edge of the foramen magnum.

The basioccipital region is extremely thickened with a pair of large anterior swellings produced from the anterior region of the occipital condyles (pl. 10, fig. 1). Weaker swellings are present in *Okapia* and *Giraffa*. Mead (1906) found that these anterior swellings are present in all horned ruminants, in which they act to strengthen the atlanto-occipital joint during combat and according to Webb (1965) they also act to prevent over flexion of the joint during grazing. The great weight of the ossicones in *Prolibytherium* would increase the requirement for such swellings for both functions. The median keel originates at the anterior end of the basioccipital and runs posteriorly, merging into the condyles between the swellings (pl. 10, fig. 1). Paired basilar tubercles lie in front of the swellings (pl. 10, fig. 1); they have sculptured surfaces and fade anteriorly into slight concavities. The tubercles provide insertion for the rectus capitis ventralis muscles which act to flex the head and to incline it laterally. The eustachian canal follows the lateral edge of the basioccipital region.

The paroccipital process is stout, with a thickened anterior face providing origin for the digastric muscle. The posterior face of the process is concave and is the area of insertion of the rectus capitis lateralis muscle. The anterior face of the process is sculptured for attachment to the meatus region of the squamosal.

Sphenoid. The optic and ethmoid foramina are more ventrally situated in *Prolibytherium* than they are in *Giraffa* or *Okapia* and the ethmoid foramen is more anteriorly situated in *Prolibytherium*. Behind the optic foramen is the large foramen rotundum (pl. 10, fig. 1) and behind this is the foramen ovale which is circular in *Prolibytherium*, as in *Giraffa* and *Sivatherium* and in contrast to *Zarafa* and the other palaeotragines in which it is oval. The orbitosphenoid is concave in front of the optic foramen. The alisphenoid has a plane lateral face and a concave ventral face, with a strong alisphenoid tuberosity at the junction of these faces. The pterygoid groove follows the edge of the basisphenoid ventro-medial to the foramen rotundum and the foramen ovale, it is roofed over at its posterior end by the temporal process of the sphenoid; this process has two longitudinal grooves on its surface, the medial one of these carries the eustachian tube and the other is continuous with the pterygoid groove. Only the posterior end of the pterygo-sphenoid is preserved. The basisphenoid is cylindrical widening slightly at the posterior end, near the suture with the basioccipital (pl. 10, fig. 1).

Squamosal. The cranial surface of the squamosal is overlapped by a downward process of the parietal and is not visible. The lateral face is convex and the postglenoid foramen is directed dorso-laterally. In front of the postglenoid foramen the bone surface is convex as far as the squamosal-alisphenoid suture. The glenoid cavity is transversely convex and the postglenoid process is slightly concave on its anterior face, the process is elongate transversely as in *Zarafa* (pl. 10, fig. 1). The temporal condyle is shallowly convex and its anterior edge forms a strong crest as far as the alisphenoid. The bone is concave medial to the glenoid cavity and a groove runs postero-laterally around the postglenoid process. The zygomatic arch is missing as the bone is broken immediately lateral to the glenoid cavity. The lateral tuberosity of the squamosal is stronger than in *Okapia*, it has a concave posterior face which is deeply sculptured. The antero-ventral face has a deep groove running laterally across it, this is the postero-dorsal part of the tube of the external auditory meatus.

Petrosal. The tympanic bulla is not preserved but the region which surrounded the bulla indicates that it was about the same relative size as that of *Okapia* or *Zarafa*. The petrosal contributes most of the meatus, with a small contribution from the squamosal in the postero-dorsal region. The meatus opens laterally as in *Okapia* or *Giraffa* and in contrast to *Capreolus* in which it slopes dorso-laterally from the bulla. The stylomastoid foramen lies postero-lateral to the meatus. Antero-ventral to the meatus is a strong hyoid process.

The inner ear is figured in ventro-lateral and medial views (text figs 5a and b). In ventro-lateral view (pl. 11, fig. 3) the most prominent region is the fossa tensor tympani, a large deep depression housing the tensor tympani muscle which inserts on the malleus. Anterior to this fossa is a deep, narrow channel, the hiatus falloppii, which carries the superficial petrosal nerve, a branch of cranial nerve VII. Posterior to the fossa tensor tympani is a small foramen which is continuous with a deep, ventrally running groove—the aquaeduct falloppii, this in turn is continuous with the stylomastoid foramen (text fig. 5a). Cranial nerve VII enters the petrosal via the

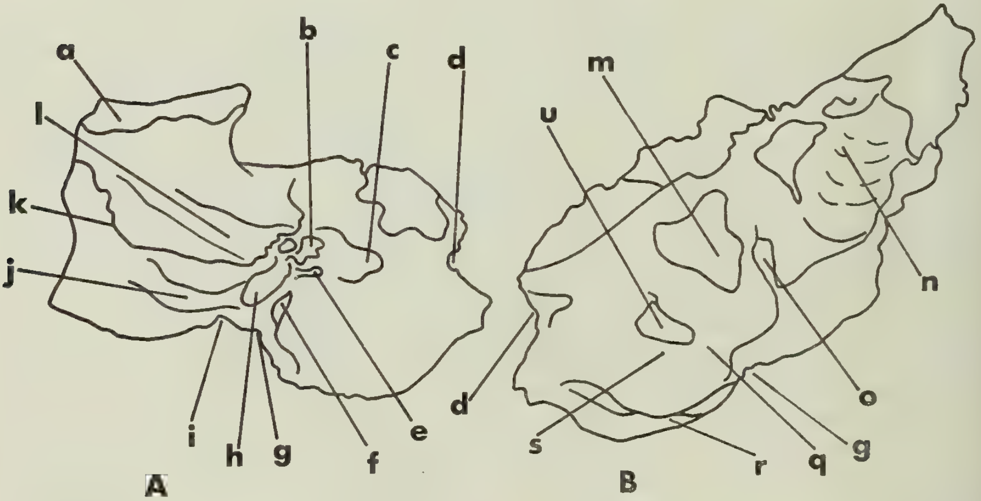

Fig. 5. The right petrosal of *Prolibytherium* (1·25 × natural size). (A) Ventro-lateral view. (B) Dorso-medial view. a: lateral tuberosity of the squamosal bone. b: aquaeduct falloppii. c: fossa tensor tympani. d: hiatus falloppii. e: fenestra ovalis. f: fenestra rotunda. g: aquaeduct cochlea. h: chorda tympani. i: groove of the foramen lacerum posterius. j: petrosal wall of the stylomastoid foramen. k: squamosal-petrosal suture. l: squamosal region of the ear. m: floccular fossa. n: wall of the temporal canal. o: aquaeduct vestibularis. q: crus commune. r: groove of the sulcus venus basilaris cranii. s: position of the semicircular canals. u: internal auditory meatus.

internal auditory meatus and after running along the aquaeduct falloppii leaves by way of the stylomastoid foramen. Postero-ventral to the fossa tensor tympani is a large opening—the fenestra rotunda, above which is the smaller fenestra ovalis (text fig. 5a). Posterior to and partly overhanging the fenestra ovalis is the stapedial promontory which provides origin for the stapedial muscle. The whole ventro-lateral face of the petrosal is very similar in *Prolibytherium* and *Capreolus*.

The medial view of the petrosal (pl. 11, fig. 4) is dominated by the internal auditory meatus which has the shape shown (text fig. 5b). Cranial nerve VII enters the petrosal posteriorly and cranial nerve VIII enters anterior to this; separate openings for the nerves are visible inside the meatus. Above and slightly behind the meatus is the wide, shallow floccular fossa which houses the floccular lobe of the cerebellum. Between the floccular fossa and the internal auditory meatus the bone is swollen by the crus commune. The semi-circular canals lie ventral to the internal auditory meatus, these were located by X-raying the petrosal but owing to the size of the specimen this technique could not be used to discover any further details of the internal anatomy.

The aquaeduct vestibularis and aquaeduct cochlea carry small veins. The medial region of the petrosal in *Prolibytherium* differs only slightly from that of *Capreolus*, the main difference being that the region around the floccular fossa and the fossa itself are more concave and larger in *Capreolus*. The petrosal of *Okapia* differs from *Prolibytherium* as the ventral part of the petrosal is expanded and the floccular fossa is relatively smaller in *Okapia*.

Brain. A single endocranial cast of *Prolibytherium* was available (pl. 12, fig. 1 and 2); this was formed from large calcite crystals and was dissected out of an almost complete cranium. The rhinal sulcus is situated very high on the lateral face of the brain (text fig. 6a); this reflects the greater importance of the rhinencephalon relative to the neopallium and is a primitive feature which is also found in *Dremotherium*, while in *Capreolus* and *Okapia* the rhinal sulcus is more ventrally situated. The anterior and posterior rhinal sulci meet each other at an angle of about 150°; this agrees with the angle given by Sigogneau (1968) for *Dremotherium*. In both *Prolibytherium* and *Dremotherium* the two regions of the rhinal sulcus join with a smoother curve whereas in *Capreolus* the anterior and posterior regions bend sharply upwards before joining. The anterior rhinal sulcus runs slightly ventrally and its anterior end is lost, due to an imperfection of the cast.

The olfactory lobes are produced anteriorly and a part of the olfactory peduncle is visible in dorsal view (text fig. 6b); this is similar to *Amphitragulus* and is more primitive than *Dremotherium* or *Capreolus* in which the olfactory peduncle is shorter and the lobes are flexed ventrally, lying under the neopallium. Posterior to the lateral fissure the brain is expanded laterally which results in a great widening of the posterior region; this is similar to *Dremotherium* but in *Capreolus* the posterior region is not expanded and in *Okapia* the brain is uniformly very wide.

The cerebellum and vermis are relatively large and lie at the same level as the neopallium; this is a primitive feature also found in *Dremotherium*. The neopallium is flattened in the vertical plane and its dorsal surface is almost flat as in *Okapia* whereas in *Capreolus* this region is curved antero-posteriorly and transversely.

The parts of the suprasylvian sulcus are clearly defined (text fig. 6a). The anterior branch curves medially with a very small descendant branch, whereas in *Capreolus* the inward curvature is more marked and a large descendant branch is produced running just in front of the sylvian sulcus. The central part of the suprasylvian sulcus is shallowly convex dorsally, this convexity is similar to *Dremotherium* but is less marked than in *Capreolus*. In *Okapia* (Clark 1939) the posterior and central parts of the suprasylvian sulcus are separated and overlap extensively. In *Prolibytherium* the posterior branch of the suprasylvian sulcus extends posteriorly almost as far as the cerebellum, it does not bifurcate whereas in *Dremotherium* a weak descendant branch is produced. A long posterior extension of the suprasylvian sulcus indicates an advance over the tragulid condition in which the posterior

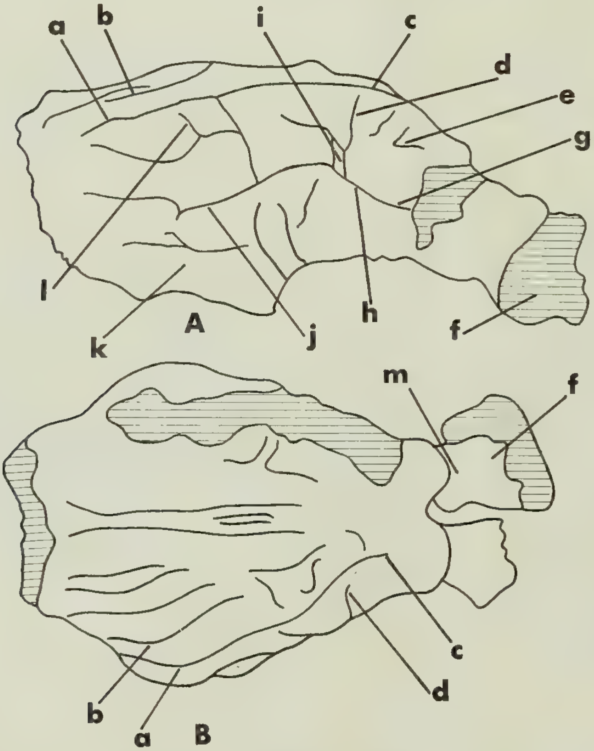

Fig. 6. The brain of *Prolibytherium* (B.M.26678) (Natural size × 0·7). (A) Right lateral view of the endocranial cast. (B) Dorsal view of the endocranial cast. a: posterior suprasylvian sulcus. b: lateral groove. c: anterior suprasylvian sulcus. d: sylvian sulcus. e: gamma sulcus. f: olfactory lobe g: anterior rhinal sulcus h: anterior ectosylvian sulcus i: lateral fissure j: posterior rhinal sulcus and posterior ectosylvian sulcus k: piriform lobe l: delta sulcus m: olfactory peduncle.

region of the sulcus is very short. The presence of a well marked descending limb of the suprasylvian sulcus, is stated by Black (1915) to be a giraffid feature and its absence in *Prolibytherium* is therefore a primitive feature.

The ectosylvian and rhinal sulci are separate near the lateral fissure but fuse completely at a short distance from the fissure both anteriorly and posteriorly, as in *Dremotherium*. This feature is primitive and in *Capreolus* and *Okapia* the rhinal and ectosylvian sulci are separate over their whole length. The lateral fissure is triangular and large (text fig. 6a) as in *Dremotherium* and *Capreolus*. The sylvian sulcus is produced from the dorsal region of the lateral fissure, this sulcus runs antero-dorsally and almost reaches the suprasylvian sulcus (text fig. 6b); this feature is similar to the cervids rather than the giraffids Clark (1939). Behind the sylvian sulcus is a deep groove which is more nearly vertical in *Capreolus* but is absent in *Dremotherium*. In *Dremotherium* the sylvian sulcus is more vertical than in *Capreolus* or *Prolibytherium*. The posterior region, between the suprasylvian and ectosylvian sulci, is occupied by the 'delta' sulcus (Sigogneau 1968); this sulcus is forked anteriorly and curves ventrally in its posterior region. The 'gamma' sulcus is very deep and much shorter in *Prolibytherium* than in *Dremotherium*.

The brain as a whole compares closely with that of *Dremotherium* but details of the sulci and olfactory lobes indicate that it was more primitive in *Prolibytherium*. The long sylvian sulcus is a cervid rather than a giraffid feature; however in *Amphitragulus* the sylvian sulcus is very short, this casts some doubt upon the importance of this feature in establishing relationships in early ruminants. As *Prolibytherium* is an early sivatheriid it is very unfortunate that no brain casts of sivatheriids were available. Agreement between the brain casts of *Prolibytherium* and the sivatheriids would probably be greater than the agreement between *Prolibytherium* and the giraffids.

Mandible. The ascending ramus is high with a concave medial and a plane lateral face in the dorsal region. The mandibular foramen is at the same level as the tooth row, it is elongate antero-posteriorly and a shallow channel runs anteriorly from it. The lower part of the ascending ramus is concave laterally and provides insertion for the masseter muscle. The horizontal ramus is convex dorso-ventrally on both sides. The ventral edge of the ramus is curved with the deepest region below M_2 (pl. 11, fig. 2). The bone surface slopes dorso-medially behind the M_3 and a sharp ridge is formed which continues dorsally as the leading edge of the ascending ramus. A small posterior mental foramen lies ventral to P_2 (pl. 11, fig. 2) in both specimens in which it is preserved. The anterior mental foramen is double in M.26680, it lies at the level of the posterior end of the symphysis and the two foramina communicate internally. The diastema of *Prolibytherium* is about the same length as the distance P_2 to M_2, which is the same as in *Capreolus* but is much shorter than in *Giraffa* or *Okapia* in which the diastema is longer than the tooth row.

Upper Dentition. The molars are generally similar in form; they are brachyodont with finely rugose enamel. M.21901 is so heavily worn that the crown of M^1 is almost completely worn away and the only remaining feature is the posterior fossette (pl. 9). The antero-labial corner of M^2 bears a strong parastyle and both the paracone and parastyle have strong labial ribs. Posterior to the paracone the wear trace is very wide but the mesostyle appears to have been originally part of the posterior lobe joining the paracone at a late stage in wear. The metacone is very stout and a slight postero-labial swelling indicates that a weak metastyle may have been present. The protocone is crescentic with the wear trace of its anterior region joining the parastyle and closing the fossette anteriorly (pl. 9). The posterior end of the protocone joins the metaconule in the median valley. The metaconule is also crescentic and is posterior end joins the metacone or possibly the metastyle thus closing the posterior fossette. At the anterior end of the metaconule is a small crest which is produced into the median valley on the lingual side of the main region of fusion between the wear traces, this crest joins the protocone enclosing a small median enamel island in M^1 and M^2 but this is not developed on M^3 (pl. 9). Each molar has a strong entostyle in the median valley; in each case this is produced from the antero-lingual region of the metaconule but on M^3 it joins a strong lingual cingulum produced from the postero-lingual face of the protocone (pl. 9). Anterior cingula are present on each molar and posterior cingula were present on M^1 and M^2.

A single badly shattered molar showing very little wear is known (P.M.F.). The mesostyle has a strong labial rib which is joined to the metacone. The metacone has a weak labial swelling and the metastyle has a strong labial rib. The protocone and metaconule are angularly crescentic and the latter is smaller than the protocone. A strong accessory crest is present in the posterior fossette.

The molars of *Prolibytherium* are smaller than those of *Zarafa*, detailed comparison is difficult owing to the heavily worn condition of the *Prolibytherium* dentition but the details of the median valley region differ between the two genera; this difference is due to the absence of the small conule in the anterior fossette of *Prolibytherium* resulting in a more simple wear pattern at the posterior end of the protocone.

P^4 is three rooted and brachyodont, it is smaller, relative to the molars and its lingual region is smaller than in *Zarafa*. The parastyle is strong with a large labial swelling and the paracone is very stout with lingual and labial ribs; the lingual rib is weaker than in *Zarafa* but it has an anterior groove as in *Zarafa* and *Palaeomeryx*. Posterior to the paracone rib, the labial wall is almost flat as far as the metastyle. The metacone is stout and almost completely fused with the paracone, its labial swelling is weak though slightly stronger than that of *Zarafa*. The protocone is stout and joins the labial lobe at both ends thus closing the fossette. The fossette of P^4 is much deeper than that of *Zarafa*, this is also true of the fossettes of the molars indicating that the upper dentition of *Prolibytherium* is much higher than that of *Zarafa*, though still brachyodont relative to the advanced giraffids or sivatheriids. At the posterior end of the fossette of P^4 is a weak accessory crest (pl. 9). The antero-lingual cingulum of the P^4 is weak relative to that of *Zarafa*.

P^2 is stout with a heavily worn crown which is concave antero-posteriorly. There are three strong ribs on the labial face which correspond to the parastyle, paracone and metacone. Between the parastyle and paracone ribs is a very deep groove (pl. 8) and a shallower groove separates the paracone and metacone ribs. No surface features are visible except a small, transversely elongate enamel island at the posterior end of the tooth.

Lower Dentition. The lower dentition forms a closed series from P_2 to M_3. The enamel of the molars is finely rugose. P.M.B. has almost unworn molars and M.26681 exhibits signs of only slight wear, these molars show that the cheek teeth are higher in *Prolibytherium* than in *Zarafa*.

M_3 has an accessory column but the anterior region differs only slightly from the other molars. The mesostylid has a strong lingual rib which runs postero-ventrally from the antero-lingual corner of the tooth (pl. 10, fig. 4). The metaconid is high and transversely compressed (pl. 10, fig. 3), its posterior end lies lingual to the anterior end of the entoconid which is lower than the metaconid and has a more diagonal orientation on the tooth (pl. 10, fig. 3). The protoconid is crescentic and slightly angular, its anterior end joins the mesostylid early in wear. The posterior end of the protoconid joins the anterior end of the entoconid early in wear (pl. 10, fig. 3) and a little later the metaconid joins the entoconid thus isolating the hypoconid until very late in wear; plate 11, fig. 1 shows a heavily worn dentition in which the hypoconid of the M_3 has just joined the protoconid. The hypoconid is lower than the protoconid, its anterior end stops in the median valley near the entoconid. The hypoconid is not crescentic in the unworn condition as the posterior region stops near the middle of the cuspid and in this region the cuspid falls away and is continued labially a few millimetres below the top of the crown; thus after moderate wear the cuspid becomes crescentic but the posterior region is always shorter and appears narrower even in the heavily worn condition. This feature is restricted to the M_3 and is related to the presence of the accessory column. The accessory column is more simple in *Prolibytherium* than in *Zarafa*; it consists of a stout hypoconulid which is as high as the hypoconid and is similar in shape to the anterior half of that cuspid. The posterior half of the hypoconulid has a weak lingual twist but there is no approach to the crescentic shape found in the giraffids. The anterior half of the hypoconulid meets the postero-labial face of the entoconid and on the lingual side of this junction is a small fold of enamel which is probably a weak ectostylid. M_3 has a feeble anterior cingulum and usually an ectostylid in the median valley.

M_1 and M_2 are similar to the anterior region of M_3. At the postero-lingual corner of M_2 is a small entostylid which joins the postero-lingual extension of the hypoconid; in all specimens the entoconid is joined to the entostylid in this region.

P_4 is long and narrow (pl. 11, fig. 1). The protoconid is the highest part of the tooth but the metaconid is almost as high, these two cuspids are joined by a narrow ridge which has a deep groove on its antero-lingual face (pl. 11, fig. 1). The anterior part of the tooth curves lingually and from the lingual face the lingual and antero-lingual paraconid and parastylid are produced; these branches are separated by a shallow lingual valley which is quickly lost during wear, leaving a single anterior region (pl. 11, fig. 1). Between the paraconid and metaconid is a deep, wide lingual valley at the lingual end of which is a strong stylid. The posterior region of P_4 consists of a stout labial hypoconid to which a postero-lingual entostylid and a lingual entoconid are joined. These two cuspids are separated by a shallow lingual valley which is lost early in wear but may persist for some time as a small enamel island. Between the protononid and the posterior region is a deep valley separating the metaconid and entoconid lingually and labially a deep groove separates the protoconid and hypoconid (pl. 11, fig. 1). A single unworn P_4 is known; on this the posterior region is entirely separated from the anterior region as the lingual and labial valleys join over the crown of the tooth. The separation of these two regions is found in the giraffids and in some palaeomerycids.

P_3 has a high protoconid with a strong postero-lingual wing—the incipient metaconid. The anterior region consists of a single wear trace derived from a paraconid and parastylid as in P_4. A lingual stylid closes the anterior valley but this is much weaker than in P_4. The posterior region is separated from the protoconid by a strong lingual valley and a weaker labial valley. The hypoconid is feeble in P_3. The entoconid is strong but the entostylid is very slender and forms the posterior face of the tooth.

The P_2 of *Prolibytherium* is a high conical tooth (pl. 11, fig. 2) of the primitive ruminant premolar form. The protoconid is high and a weak postero-lingual fold represents the metaconid. Anteriorly the paraconid consists of an unbranched crest which runs anteriorly from the face of the protoconid (pl. 11, fig. 1) and twists lingually at the distal end. The posterior region is transversely wide with a weak entoconid and entostylid. This tooth is similar that of *Palaeotragus rouenii* but in this species the anterior crest is divided into a parastylid and a paraconid which is a more advanced condition.

The Skull as a Whole. The dorsal view of the skull is dominated by the enormous ossicones which are completely fused to the frontal and parietal bones. The great thickening of the basioccipital region and the occipital condyles is directly related to the presence of the ossicones. Though the facial region is poorly known it is of great interest as a lacrymal fossa and paired lacrymal foramina are present, these are primitive features previously unrecorded in the Giraffoidea but similar to the cervoid or dremotherioid condition. The maxilla is shallow as in *Capreolus* and it is likely that the basicranial and basifacial regions were widely divergent as in *Zarafa*. The endocranial cast shows similarities to the dremotherioids. In most features the skull of *Prolibytherium* is similar to the early pecorans but this resemblance is decreased by the presence of the ossicones in *Prolibytherium*.

TABLE 8

Prolibytherium magnieri. Measurements of the skull and dentition

The Skull

	B.M.21901
Postorbital length. (From anterior edge of orbit to occipital condyle)	132 mm
Width of ossicones above the orbit	320 mm
Maximum length of the ossicones	425 mm
Width of condyles	51 mm
Height of occipital region	71 mm
Height of occipital region plus ossicones	114 mm
Maximum width of occipital region	93 mm

The Upper Dentition

	B.M.21901	
	Length	Width
P^2	12·5 mm	9·0 mm

TABLE 8 (*cont.*)

P^4	11·0 mm	14·0 mm
M^1	15·0 mm	17·5 mm
M^2	18·0 mm	20·0 mm
M^3	20·0 mm	20·0 mm

The Lower Dentition

	M.21899	M.26681	B.U.20175	P.M. A.	P.M. B.	P.M. C.	P.M. D.
P_2							
Width	5·3 mm	—	—	—	—	—	—
Length	10·0 mm	—	—	—	—	—	—
P_3							
Width	6·5 mm	—	—	7·0 mm	—	—	—
Length	11·0 mm	—	12·0 mm	12·0 mm	—	—	—
P_4							
Width	8·5 mm	—	9·0 mm	7·5 mm	—	7·5 mm	—
Length	13·0 mm	—	14·5 mm	12·8 mm	—	13·5 mm	—
M_1							
Width	12·0 mm	—	12·0 mm	12·0 mm	—	—	11·5 mm
Length	13·0 mm	—	15·0 mm	13·5 mm	14·0 mm	—	16·5 mm
M_2							
Width	12·5 mm	—	13·0 mm	13·0 mm	—	—	13·0 mm
Length	16·5 mm	—	—	18·5 mm	18·5 mm	—	17·5 mm
M_3							
Width	12·0 mm	13·0 mm	13·0 mm	12·5 mm	—	—	13·0 mm
Length	23·5 mm	26·5 mm	26·5 mm	24·5 mm	25·0 mm	—	25·0 mm

Post-cranial material. Details of the skull indicate that *Prolibytherium* was probably similar to the more primitive cervids and it is therefore likely that its post-cranial material resembled that of the cervids. On this basis the post-cranial material of *Prolibytherium* was identified by comparison with a skeleton of *Capreolus*.

MATERIAL

B.U.20153	A proximal fragment of a left scapula.
B.U.20154a	The distal end of a left humerus.
b	A complete left radius.
c	The proximal end of a left ulna.
B.U.20155	The distal end of a metacarpal.
B.U.20156	A first phalange.
B.U.20157	A first phalange.
B.U.20158	A first phalange; posterior?
B.U.20159	The proximal end of a right tibia.
B.U.20160	The proximal end of a left tibia.
B.U.20161	The distal end of a right tibia.
B.U.20162	The distal end of a left tibia.
B.U.20164	A right calcaneum.
B.U.20165	A right astragalus.
B.U.20166	A right astragalus.
B.U.20167	A left astragalus.
B.U.20168	A right astragalus.

B.U.20169	A distal, metatarsal fragment.
B.U.20170	An almost complete atlas vertebra.
B.U.20171	A slightly broken seventh cervical vertebra.
B.U.20172	A complete first thoracic vertebra.
B.U.20173	An almost complete thoracic vertebra.

Scapula. The glenoid region of the scapula has an almost circular outline with a small glenoid notch (text fig. 7a). The coracoid process is strong but the tuber scapulae is weak. The spine begins near the glenoid and rises steeply indicating the presence of a strong acromion process. The neck of the scapula is wider than in *Zarafa* or *Okapia*; it has a deep vascular groove on the medial surface and a strong tuberosity on the posterior edge which is the area of origin for the teres minor muscle. The outlines of the glenoids in four giraffoid genera (text fig. 7) demonstrate the differences which exist in the development of the coracoid process and the tuber scapulae. The tuber scapulae of *Prolibytherium* (text fig. 7a) is very feeble, in *Zarafa* it is stronger (text fig. 7c) and in the extant giraffids it is very strong (text fig. 7b and d). The coracoid process is strongly developed in *Prolibytherium* and weakly developed in the giraffids indicating that in *Prolibytherium* the coraco-brachialis muscle was more highly developed than in the giraffids. The neck of the scapula indicates that the bone was shorter and wider than that of *Okapia* and probably resembled the scapula of *Ovis.*

Humerus. The coronoid fossa is much deeper than in *Okapia* or *Giraffa*; this fossa provides origin for the extensor carpi radialis and the common digital extensor muscles, both of which were strongly developed in *Prolibytherium.* The lateral condyle is narrow with a transversely concave face, this concavity is caused by very strong lateral and intermediate ridges. The intermediate ridge separates the

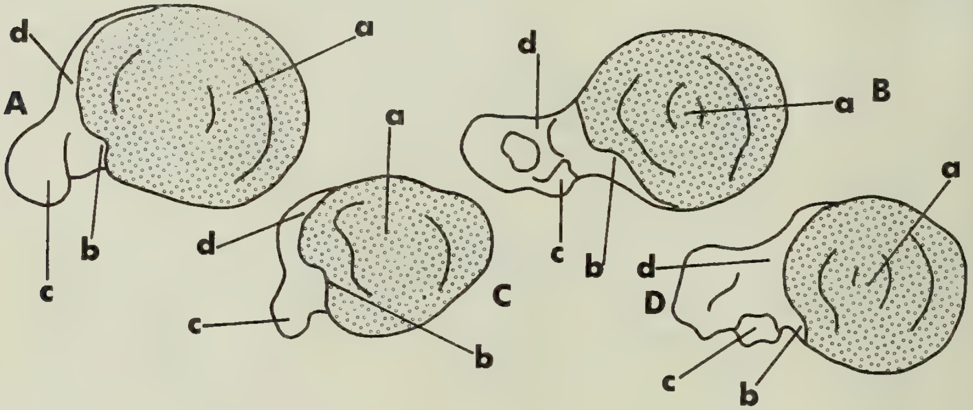

Fig. 7. The glenoid cavity and surrounding region of the left scapula. (A) *Prolibytherium* (B.U.20153) Natural size. (B) *Okapia* 0·5 × Natural size. (C) *Zarafa* (B.U.20123) 0·5 × Natural size. (D) *Giraffa,* 0·25 × Natural size. a: glenoid cavity. b: glenoid notch. c: coracoid process. d: tuber scapulae.

condyle from the synovial fossa and all the ridges of the distal head of the humerus are much stronger than in *Okapia*. The olecranon fossa is very deep and the articular region extends further into the fossa than in *Okapia*. The medial epicondyle is very strong, it is produced distally as a large process overhanging the medial condyle (text fig. 8a). The medial condyle of *Okapia* is more weakly developed than that of *Prolibytherium* and slopes proximally from the condyle (text fig. 8b). The medial, distal and lateral faces of this epicondyle are very heavily sculptured in *Prolibytherium* and the main digital flexor muscles have areas of origin on this epicondyle. The lateral epicondyle of *Prolibytherium* is slightly stronger than that of *Okapia*, this region provides origin for the ulnaris lateralis muscle.

Radius. The central part of the proximal face of the radius is deeply excavated posteriorly for the insertion of the interosseous ligament. This excavation is about the same size in *Prolibytherium* and *Okapia* (text fig. 9). The postero-proximal region of the bone is sculptured for attachment to the ulna and this region bears two wide concave facets which are continuous with the proximal facets and articulate with the ulna. The lateral part of the proximal region forms a strong lateral tuberosity providing insertion for the lateral ligament of the elbow and also origin for the common lateral digital extensor muscles. The radial tuberosity, about the same size in *Prolibytherium* and *Okapia*, provides insertion for the biceps brachii muscle. In *Prolibytherium* it is situated at some distance distal to the articulation in contrast to *Okapia* in which the tuberosity is very near the articulation (text fig. 9).

The shaft of the radius is slender and curved anteriorly as in *Okapia* and *Capreolus*. The distal end is transversely narrower than in *Okapia*; it has the usual articulations

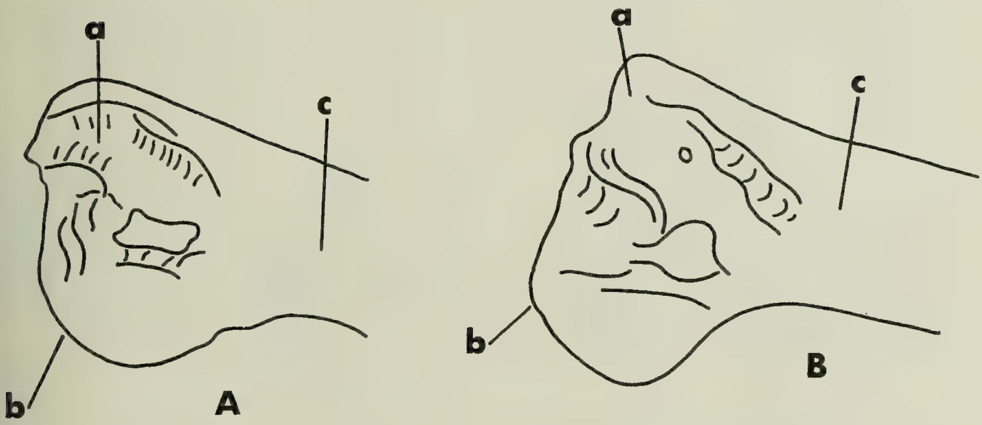

FIG. 8. Medial view of the distal end of the humerus. (A) *Prolibytherium* (B.U.20154a). Natural size. (B) *Okapia* 0·5 × Natural size. a: medial epicondyle. b: medial condyle. c: shaft of humerus.

for the carpals. The area lateral to the cuneiform facet is sculptured indicating a very close attachment of the ulna in this region. In *Prolibytherium* the posterior face of the radius is convex in the region immediately proximal to the distal facet; this contrasts with *Okapia* in which this face is concave. The lateral tuberosity of the distal end is strong and the medial tuberosity is stronger in *Prolibytherium* than in *Okapia*; these tuberosities provide insertion for the ligaments of the carpal joint.

Ulna. The olecranon process is flattened and though it is broken off distally it was probably as long as that of *Okapia.* The shaft of the ulna is also flattened transversely and bends medially at its distal end as in *Okapia.* The interosseous space is short and relatively narrow. In *Prolibytherium* the articular facet is convex transversely, in contrast to *Okapia* in which the facet is flat transversely. The greater convexity of the facet reflects the deeper synovial fossa and stronger ridges of the distal end of the humerus. The facet of the olecranon in *Prolibytherium* extends further dorsally than in *Okapia* resulting in a more elongate facet and at full extension the olecranon fits into the deep olecranon fossa and locks the elbow.

Metacarpal. The distal end of the metacarpal has a large nutrient foramen in the mid-line proximal to the condyles as in *Zarafa.* The distal end of the bone is wide and indicates that the metacarpal was relatively stout. The condyles are of the usual ruminant pattern with strong keels as in the cervids.

Tibia. In *Prolibytherium* the proximal head of the tibia is narrower than that of *Okapia* but is otherwise similar in general anatomy. The cnemial crest is higher in *Prolibytherium* than in *Okapia* or *Zarafa* (text fig. 10) resembling that of *Capreolus.* The medial face of the cnemial crest is plane and the anterior region of the crest is

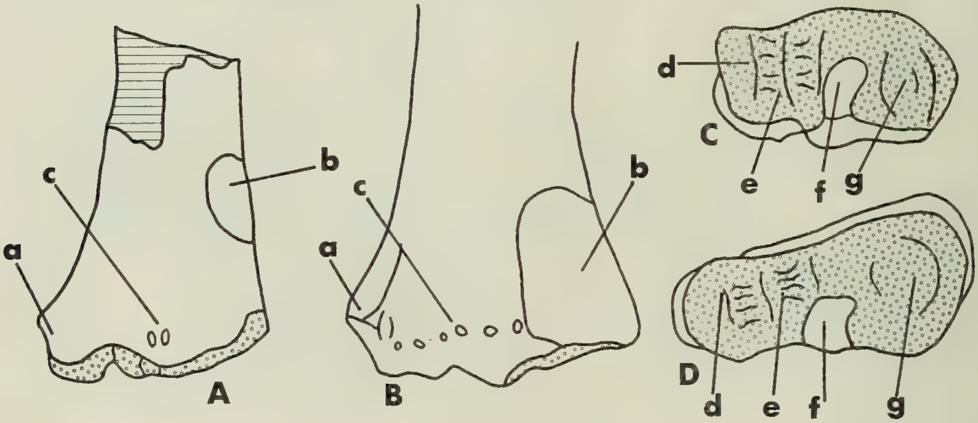

FIG. 9. The radius of *Prolibytherium.* (A) The anterior face of the proximal region of the radius in *Prolibytherium* (B.U.20154b). Natural size. (B) The anterior face of the proximal region of the radius in *Okapia.* 0·5 × Natural size. (C) The proximal articular facet of the left radius in *Prolibytherium.* Natural size. (D) The proximal articular facet of the left radius in *Okapia.* 0·5 × Natural size.

heavily sculptured. The anterior tuberosity of the crest is wide and similar to that of *Capreolus*. The lateral face of the crest forms a deep elongate concavity which is deeper than that of *Okapia* or *Capreolus*.

The distal end of the tibia is narrow transversely. The medial articular groove is very deep and the intermediate ridge is high resembling that of *Zarafa* or the cervids. The anterior edge of this ridge continues as a high anterior process. The synovial fossa is large and extends laterally and medially into the articular grooves. The articulation for the lateral malleolus consists of a wide posterior facet and a smaller anterior facet as in *Zarafa*. The anterior and posterior facets are separated by a deep groove for the tendons of the lateral extensor muscles of the foot. The medial malleolus is heavily sculptured and as strong as in *Okapia*.

Calcaneum. The calcaneum differs in minor details from that of *Palaeomeryx* but in major features it is more similar to *Palaeomeryx* than to any other giraffoid.

Astragalus. In agreement with the calcaneum the astragalus of *Prolibytherium*

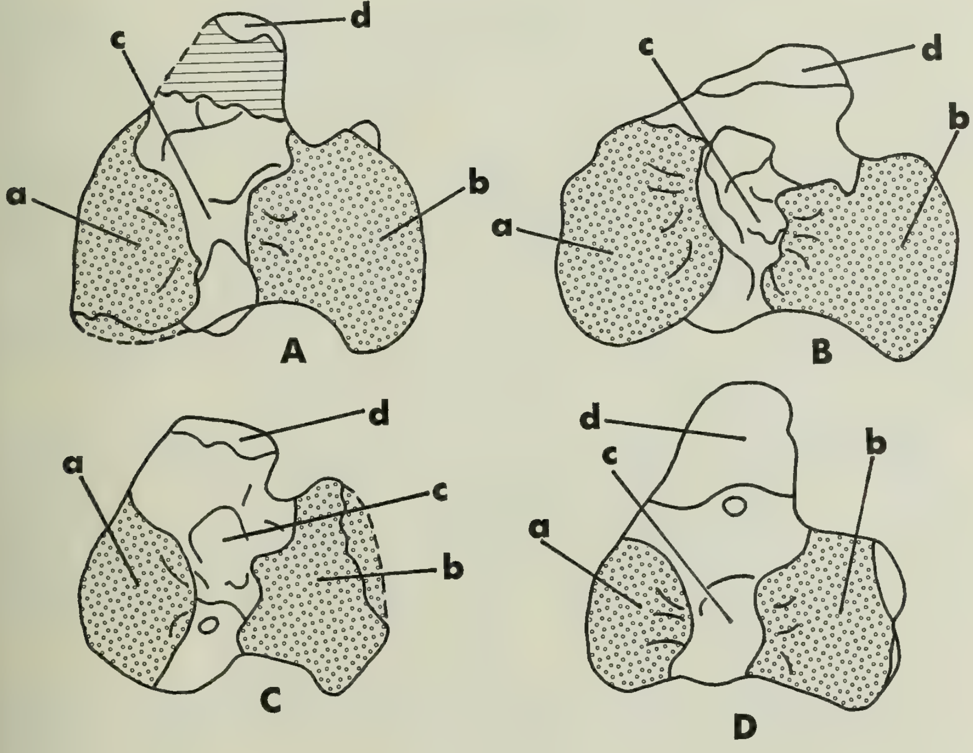

FIG. 10. The proximal head of the right tibia. (A) *Prolibytherium*. (B.U.20159 and B.U.20160). Natural size. (B) *Okapia* 0·5 × Natural size. (C) *Zarafa* (B.U.20146) 0·5 × Natural size. (D) *Capreolus* Natural size. a: medial condyle. b: lateral condyle. c: tibial spine. d: cnemial crest.

resembles that of *Palaeomeryx* in all its main features. Both the astragalus and calcaneum contrast strongly with those of *Okapia* but this is mainly due to the specialized nature of the ankle in *Okapia*.

Metatarsal. This bone is larger than the metacarpal; the reverse of the condition in *Okapia* and *Giraffa* but similar to the cervid condition. The distal end is more flattened antero-ventrally than in *Okapia* or *Zarafa*. The anterior face of the bone carries a deep channel which is open and passes between the condyles, this channel is very restricted in the region just proximal to the condyles and the walls of the channel are sculptured as in *Zarafa*. The condyles are similar to the cervids or *Zarafa*.

Phalanges. The phalanges identified as *Prolibytherium* are smaller than those of *Zarafa* but are otherwise similar in all details and reference should be made to the description of *Zarafa* (p. 97).

THE VERTEBRAL COLUMN

Atlas. The atlas of *Prolibytherium* (text fig. 11c and d) is identified by its size which agrees with the size of the occipital condyles. The general form of the atlas is similar to that of other ruminants. The anterior articular facets are very deep and their lateral curvature is sharper than in *Okapia*, agreeing with the condition of the occipital condyles. The wing of the atlas is broken off. The intervertebral and alar foramina are closely associated ventrally and dorsally they have a common opening (text fig. 11c) as in *Capreolus* but in contrast to *Okapia* where they are widely separated. The ventral face of the atlas is similar to that of *Okapia* and the ventral tubercle is very strong (text fig. 11d). The posterior articular facets are swollen medially and concave laterally, differing from *Okapia* in which the facets are more nearly plane. In *Prolibytherium* the posterior articular facet extends further laterally than that of *Okapia* and as in *Giraffa*, it is continued onto the postero-lateral process of the wing. Although this process is broken off it appears to have been as strong as that of *Giraffa*, indicating a strengthening of the atlanto-axis articulation in *Prolibytherium*. The bone of the atlas is very thick.

Cervical vertebrae. The centrum of the seventh cervical vertebra (text fig. 11a) is stouter than that of *Okapia* and has a strong ventral ridge. The anterior end of the centrum is displaced dorsally relative to the posterior end but less so than in *Okapia*. On the posterior face the lateral facet for the head of the rib is wider and more clearly defined than in *Okapia*. The posterior articular process is lateral only and the articular facet is more elongate in *Prolibytherium* than in *Okapia* (text fig. 11a). The anterior articular process is similar to that of *Okapia* with similarly shaped facets. The transverse processes and neural spine are broken off.

Thoracic vertebrae. The centrum of the first thoracic vertebra is very short and stout. The anterior facet of the centrum (text fig. 11g) is shallowly convex and the facets for the head of the rib (text fig. 11f) face much more anteriorly than in *Okapia*. The posterior facet of the centrum is shallowly concave with wide lateral facets for the heads of the ribs (text fig. 11e). The ventral face of the centrum is not greatly swollen. A small tubercle is produced at the anterior end of the ventral face and the paired posterior tubercles are very laterally situated. The transverse process is strong and the saddle shaped articulation for the tubercle faces ventrally (text fig. 11f) whereas in *Okapia* it faces antero-ventrally. The anterior articular process is similar to that of *Okapia*, with wide lateral articulations extending further medially than in *Okapia*. The articulation of the posterior process is median in *Prolibytherium* and the paired facets are well defined (text fig. 11e); they are elongate, narrow and opposed at an acute angle as in *Giraffa*. The neural spine slopes more posteriorly than in *Okapia*, it is the same relative length in *Prolibytherium* and *Okapia*. The

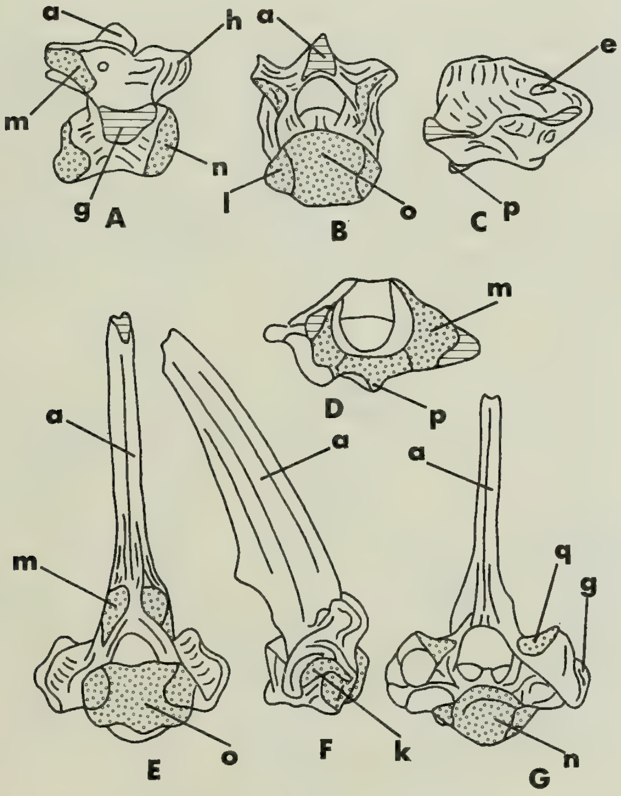

Fig. 11. The vertebrae of *Prolibytherium*. (A and B) Lateral and posterior views of the seventh cervical vertebra. (B.U.20171). (C and D) Lateral and posterior views of the atlas (B.U.20170). (E, F and G) Posterior, lateral and anterior views of the first thoracic vertebra. (B.U.20172). All 0·5 × Natural size. Fine stippling indicates articular regions. a: neural spine. e: common dorsal opening of the intervertebral and alar foramina. g: transverse process. h: anterior articular process. k: tubercular facet. l: posterior facet for the head of the rib. m: posterior articular facet. n: anterior face of centrum. o: posterior face of centrum. p: ventral tubercle.

cross-section of the neural spine is triangular with thickening of the posterior edge and heavy sculpturing in the region just dorsal to the posterior articular process.

A single vertebra is known from the posterior thoracic region of *Prolibytherium*, this is probably the tenth or eleventh thoracic vertebra. The neural spine is stronger than in *Okapia* and it slopes more steeply posteriorly. Both faces of the centrum and the anterior and posterior articular processes of *Prolibytherium* are similar to those of *Giraffa*.

Functional interpretations. Features of the fore-limb bones of *Prolibytherium* indicate that the locomotory muscles were very strong and a requirement for strength rather than speed is indicated. The animal had relatively short limbs probably not unlike those of *Ovis*. The presence of large ossicones would have necessitated great strength in the forelimbs and if the ossicones were used in intraspecific combat, as seems likely, then this requirement for strength would be exaggerated.

Details of the skull and atlas vertebra indicate that great forces were encountered by the head of *Prolibytherium*. The lower cervical region is represented by the seventh cervical and first thoracic vertebrae. If the neural spine of the seventh cervical vertebra was vertical during life, then the neck extended almost horizontally from the shoulders and it is likely that the head did not rise much above the level of the shoulders. The stoutness of the centra of the lower neck vertebrae and the shortness of the atlas indicate that the neck was short and probably very stout.

TABLE 9

Measurements of *Prolibytherium magnieri*, post-cranial material

Vertebrae

	B.U.20170	B.U.20171	B.U.20172	B.U.20173
Length of centrum	28 mm	30 mm	23 mm	27 mm
Total height of vertebra	34 mm	—	102 mm	—
Depth of centrum	—	19 mm	18 mm	16 mm
Width of anterior end of centrum	—	15 mm	19 mm	22 mm
Width of posterior end of centrum	—	27 mm	29 mm	30 mm

Scapula

	B.U.20153
Width of neck of scapula (Minimum)	25 mm
Depth of neck of scapula (Minimum)	14 mm
Width of glenoid (Anterior-Posterior)	30 mm
Depth of glenoid (Transverse)	25 mm

Humerus

	B.U.20154a
Distal end	
Width across epicondyles	35 mm
Antero-posterior depth of distal articular surface	18 mm

Radius

	B.U.20154b
Width of proximal articular surface	35 mm

TABLE 9 (*cont.*)

Depth of proximal articular surface:	
Minimum	13 mm
Maximum	18 mm
Total length of bone	210 mm
Width of distal articular surface	29 mm
Depth of distal articular surface	21 mm

Metacarpal

	B.U.20155
Width of distal end	27 mm
Depth of distal end	15 mm

Phalanges

	B.U.20156	B.U.20157	B.U.20158
Length	37 mm	37 mm	33 mm
Width of proximal end	13 mm	14 mm	13 mm
Depth of proximal end	14 mm	14 mm	14 mm
Width of distal end	11 mm	11 mm	10 mm
Depth of distal end	09 mm	09 mm	09 mm

Tibia

	B.U.20159	B.U.20160	B.U.20161	B.U.20162	B.U.20163
Width of proximal end	47 mm	46 mm	—	—	—
Depth of proximal end	46 mm	44 mm	—	—	—
Width of distal end	—	—	29 mm	27 mm	30 mm
Depth of distal end	—	—	21 mm	21 mm	23 mm

Calcaneum

	B.U.20164
Total length	70 mm
Length of tuber calcis	48 mm
Width across sustentaculum	19 mm
Depth of tuber calcis	18 mm
Maximum depth of bone	28 mm

Astragalus

	B.U.20165	B.U.20166	B.U.20167	B.U.20168
Maximum length	32 mm	36 mm	33 mm	33 mm
Minimum length	26 mm	30 mm	26 mm	25 mm
Width proximally	20 mm	20 mm	20 mm	18 mm
Width distally	18 mm	20 mm	19 mm	18 mm
Maximum depth	15 mm	16 mm	16 mm	15 mm

Family **BOVIDAE** Gray 1821.

Subfamily **BOVINAE** Gill 1872.

DIAGNOSIS: This subfamily is defined by Pilgrim (1939 p. 249).

Tribe **BOSELAPHINI** Simpson 1945.

DIAGNOSIS: This tribe is defined by Gentry (1970 p. 245).

Genus ***PROTRAGOCERUS*** Depéret 1887

TYPE SPECIES: *Protragocerus chantrei* Depéret 1887.

MATERIAL:

M.26687	An isolated right horn core fragment.
B.U.20113	An isolated left horn core fragment with part of the frontal attached.
B.U.20114	An isolated right horn core fragment.

DESCRIPTION: M.26687 (pl. 13, fig. 1) is the best preserved of the three specimens; part of the orbital region is preserved in the ventro-lateral region of the specimen and in the medial part of the orbital roof a small supraorbital foramen runs dorso-medially for a short distance in the bone, before turning anteriorly to emerge in the antero-medial region of the horn core, as in *Protragocerus gluten.* The lateral region of the orbit extends slightly more laterally than the lateral face of the pedicle, which results in a weak lateral swelling in this region; however the horn core is more laterally situated than in *Protragocerus gluten* which may indicate that the Gebel Zelten species is more primitive. The region of the frontals lying between the bases of the horn cores, is slightly higher than the edge of the orbit and in B.U.20113 the area immediately medial to the horn core base is concave as far as the median suture, which is strong and slightly raised.

The horn core is set diagonally on the skull roof and in B.U.20113 it slopes laterally at an angle of about 20° from the vertical; however in M.26687 this angle is smaller. The horn core also slopes posteriorly at an angle of 35° in all three specimens; which is very similar to the posterior slope in *Protragocerus gluten* (Pilgrim 1937). The surface of the horn core carries many pronounced vertical ridges and grooves which terminate a short distance above the skull roof, there are no cross striations.

The anterior and posterior keels are strong but do not show any signs of the torsion exhibited by more advanced forms. There is no medial keel but the medial face of the horn core is convex antero-posteriorly and a slight swelling may be detected near the middle of the face, this could be an incipient third keel. The medial face is concave proximo-distally, which indicates that the horn cores, though divergent at their bases, may have become more convergent distally. The lateral face is convex proximo-distally at the base but shows slight concavity distally. The cross-section of the horn core agrees closely with that of *Protragocerus gluten* (Pilgrim 1937) and the agreement with *Protragocerus chantrei* (Thenius 1956) is more distant. On the basis of this evidence the horn cores from Gebel Zelten, although more primitive than other specimens of *Protragocerus,* do exhibit features which indicate their close relationship and also incipient features which could lead to the characteristics exhibited by the more advanced species of the genus.

In B.U.20113 sufficient of the roof is preserved for an estimate of the width across the orbits to be made, this was certainly not greater than 6·5 cm and not less than 6·0 cm which is much smaller than *Protragocerus gluten* and indicates an animal in the same size range as the small mandible which has been identified as *Gazella* sp. The features of the horns and mandible which separate them into different sub-families are very conclusive and the chances that these two specimens could be from the same species are very small indeed.

Genus **EOTRAGUS** Pilgrim 1939

Diagnosis: The genus *Eotragus* is defined by Pilgrim (1939 p. 137).

Type species: *Eotragus haplodon* (von Meyer) 1846.

Eotragus sp.

Material:

M.26688	A single isolated horn core.
M.26689	A single isolated horn core.

Description: The supraorbital foramen penetrates the roof of the orbit and the canal curves inside the bone, to open on the anterior face of the horn core base near the centre of the base. The horns were almost vertical and perhaps slightly convergent; they were situated supraorbitally and were very near the edge of the orbit. The surface of the horn core is excavated by a large number of proximo-distal grooves but transverse grooves are totally absent (pl. 13, fig. 1). A strong keel is present on the posterior face of the horn core; this keel is stronger in M.26689 than it is in M.26688 but as the latter is from an older individual the strength of the keel may have decreased with age. The cross-section of the horn core agrees closely with that of *Eotragus sansaniensis* (Thenius 1952 fig. 5). The lateral face is convex proximo-distally agreeing with *Eotragus haplodon* (Thenius 1952) and the Gebel Zelten specimens also agree in size with this species; however the horns were certainly longer in the Gebel Zelten species than in *E. haplodon* as the opposing faces converge more gradually in the former species.

Table 10

Horn cores

	Protragocerus		*Eotragus*	
	B.M.26687	B.U.20113	B.M.26688	B.M.26689
Maximum antero-posterior thickness of horn core	27·8 mm	—	20·6 mm	16·9 mm
Maximum antero-posterior thickness of pedicle	25·5 mm	25·7 mm	19·4 mm	16·7 mm
Maximum transverse width of horn core	18·0 mm	—	17·1 mm	14·3 mm
Maximum transverse width of pedicle	17·7 mm	—	17·0 mm	15·5 mm

Subfamily **ANTILOPINAE** Baird 1857

Diagnosis: The subfamily was defined under the name Gazellinae by Pilgrim (1939 p. 30).

Genus ***GAZELLA*** De Blainville 1816

Diagnosis: The genus was defined by Gentry (1970 p. 292).

Gazella sp.

REMARKS: Species of *Gazella* are identified as much on the basis of the horn cores and occipital region as by the dentition. The confused state of classification within the genus is being gradually resolved (Gentry 1964, 1966, 1970) but at the moment the material from Gebel Zelten is insufficient to identify the specimen with any existing species or to allow the establishment of a new species.

MATERIAL:

M.26685	An isolated left mandible, dentition showing medium wear.
M.26686	A left mandibular fragment, M_3 partially erupted.

Mandible. The mandible is clearly bovid and the dentition confirms this. For purposes of comparison mandibles of *Gazella capricornis* and *G. pilgrimi* were used: with reference to the former Gentry (1970) states:

> '*Gazella capricornis* (Wagner) is the gazelle of the famous Pikermi lower Pliocene fauna from Attica. . . . Its teeth frequently show primitive characters: basal pillars on other teeth than the upper and lower first molars, strong ribs between parastyle and mesostyle of upper molars, medial wall of lower molars not very flattened, fairly shallow mandibular horizontal rami, and probably a longer premolar row.'

The species *G. pilgrimi*; with which Gentry synonymized *G. gaudryi*; is a more advanced form from Samos in which the dentition lacks primitive characters.

In the Gebel Zelten species the mandible is deep with the deepest point lying below the anterior end of M_3. The lateral face of the mandible is convex with a strong swelling in the posterior region as in *Sylvicapra.* A small posterior mental foramen lies below the anterior end of P_2. The anterior mental foramen is very large and double as in *Sylvicapra.* The diastema is short and though the anterior region is missing its length was probably similar to that of *Gazella* or *Sylvicapra.* The medial face of the mandible (pl. 13, fig. 8) is convex dorsally but a shallow concavity runs antero-posteriorly along the ventral part of this face. The mandibular foramen is large and below it is a shallow mandibular groove as in *Gazella.*

Lower dentition. The molars of the Gebel Zelten species are more brachyodont than in *G. capricornis* or *G. pilgrimi* and cingula are lacking in all three species. On M_3 the mesostylid is as strong as that of *G. capricornis* but is weaker than in *G. pilgrimi.* The metaconid is high, transversely flattened and set diagonally on the tooth causing the metastylid to be produced lingually. In *G. capricornis* the lingual cuspids are parallel to the axis of the tooth. The metaconid has a weak lingual swelling. The metastylid is very weak and is lost after medium wear. The entoconid is as high as the metaconid and has a more feeble lingual swelling, it is set more nearly parallel to the axis of the tooth than the metaconid. The protoconid is high and crescentic with no trace of a '*Palaeomeryx* fold', its anterior region joins the mesostylid very early in wear. The posterior end of the protoconid meets the metaconid and entoconid at the lingual end of the median valley. The hypoconid is lower than the protoconid but is less isolated than in the palaeomerycids. The posterior end of the hypoconid joins the entoconid, isolating the hypoconulid which forms the accessory column; this is lower than the hypoconid and is crescentic, resembling closely the accessory column of *G. capricornis* or *G. pilgrimi*. Excluding the differences mentioned the M_3 of the Gebel Zelten species is very similar to the two European species.

M_2 resembles the anterior region of M_3. The mesostylid is stronger in M_2 than in M_3 (pl. 13, fig. 2), this may be a compensatory strengthening as the metaconid is more nearly parallel to the axis of the tooth in M_2. M_1 is more worn but otherwise similar to M_2. Each molar has a strong ectostylid and M_3 has a weak stylid in the posterior valley, these stylids are similarly developed in *G. capricornis*.

The P_4 of the Gebel Zelten species is short with a high protoconid which gives off a strong postero-lingual metaconid. The anterior region consists of a paraconid which is stout and directed antero-lingually. A parastyle does not appear to have been developed as the lingual face of the paraconid does not bear a groove (pl. 13, fig. 2). The posterior region is wide and the hypoconid is stout with a strong labial swelling (pl. 13, fig. 2) which is separated from the protocone by a deep labial groove. The entoconid is strong and wide but it is heavily worn and the presence of an entostylid cannot be established; the absence of a lingual groove on the face of the entoconid(pl. 13, fig. 3) indicates that an entostylid was probably not present.

The P_4 of *G. capricornis* is similar to that of the Gebel Zelten species. The hypoconid is strong in *G. capricornis* and has a strong labial swelling as in *Gazella* sp.. The metaconid, entoconid and entostylid are similar in the two species but the anterior regions differ as the paraconid and parastylid are widely separated in *G. capricornis* but are joined in *Gazella sp.*. The P_4 of *G. pilgrimi* is smaller than in *Gazella sp.* and the hypoconid is more feebly developed. The entoconid and entostylid are more widely separated in *G. pilgrimi* than in *Gazella* sp. and, as in *G. capricornis*, the paraconid and parastylid are also widely separated in *G. pilgrimi*.

The P_3 is much shorter than the P_4 (table 11); the lingual region is badly broken (pl. 13, fig. 3). The labial wall has a strong hypoconid swelling as in P_4. The P_3 of *G. capricornis* is highly developed and is as long as the P_4 (table 11); its paraconid and parastylid are strongly separated as on the P_4 and in contrast to the P_3 of *Gazella* sp. in which the anterior region is not divided. The P_3 of *G. pilgrimi* is smaller than that of *Gazella* sp. but the paraconid and parastylid are separated as in *G. capricornis*. The P_2 is missing in M.26685 but it appears to have been greatly reduced in length and was probably comparable to the P_2 of *G. pilgrimi* or *G. capricornis*.

The molars of the Gebel Zelten gazelle are therefore similar to those of the European Pliocene species and they were similar in length and width to those of *G. capricornis*; however in that species the molars are more hypsodont than in *Gazella sp.* and even after medium wear the molars of *G. capricornis* are almost as high as the unworn dentition of M.26686. The molars of *G. capricornis* are more advanced than those of the Gebel Zelten gazelle. The premolar row is relatively long in *G. capricornis* and short in *Gazella sp.* and *G. pilgrimi*; thus in this respect *Gazella sp.* resembles the more advanced *G. pilgrimi*. It is not possible to place the Gebel Zelten gazelle with either of these species as it shows features which are present in both species and also exhibits some features such as degree of brachyodonty and details of the premolars, which are more primitive than in either species.

TABLE II

	Gazella sp. B.M.26685		*Gazella sp.* B.M.26686		*G. pilgrimi* B.M.4177		*G. capricornis* B.M.13014	
	Length	Width	Length	Width	Length	Width	Length	Width
P_2	5·0 mm	—	—	—	4·7 mm	2·7 mm	5·2 mm	3·7 mm
P_3	7·2 mm	4·0 mm	—	—	5·7 mm	3·7 mm	9·5 mm	5·2 mm
P_4	8·6 mm	5·5 mm	—	—	7·3 mm	4·5 mm	9·7 mm	5·4 mm
Total length of premolar row	20 mm				17·7 mm		24 mm	
M_1	9·5 mm	6·7 mm	—	—	9·1 mm	5·0 mm	10·0 mm	5·6 mm
M_2	11·0 mm	7·0 mm	—	—	10·0 mm	6·0 mm	10·6 mm	6·4 mm
M_3	14·6 mm	6·6 mm	15·0 mm	6·8 mm	14·5 mm	6·7 mm	14·7 mm	6·6 mm
Total length of molar row	34·4 mm				32·1 mm		34·0 mm	
% Premolar to Molar length (Molar length—100)	58·1%				55·1%		70·6%	
Maximum height from neck to top of crown								
P_3	5·9 mm		—		—		7·5 mm	
P_4	6·8 mm		—		—		7·7 mm	
M_1	7·0 mm		—		—		8·0 mm	
M_2	8·3 mm		9·1 mm		—		9·1 mm	
M_3	9·0 mm		10·5 mm		—		9·6 mm	

The presence in the Zelten fauna of three species of bovids in the early Burdigalian is surprising as, with the exception of European sites and the Hsanda Gol of Asia, bovids are of later occurrence. The presence of three bovid genera representing the two most important subfamilies of the Bovidae indicates that the bovids were already well established in the early Miocene and therefore they must have diverged from their ancestral stock at some time during the Oligocene. The presence of bovids at Hsanda Gol is not yet well established though Trofimov (1968) figures very bovid like lower molars of *Palaeohypsodontus* and this may indicate that the ancestry of the bovids must be sought in the Oligocene of Asia.

III. THE EVOLUTION OF PRIMITIVE GIRAFFOIDS

The Giraffoidea was established by Simpson (1931) to include the Palaeomerycidae and Giraffidae; Simpson (1945) demoted the Palaeomerycidae to subfamily level and transferred it to the Cervoidea, leaving the Giraffoidea containing the Giraffidae and the Lagomerycidae.

The Palaeomerycidae was established by Lydekker (1883) taking its name from *Palaeomeryx* von Meyer 1834. *Lagomeryx* Roger 1904, was established to include small species of *Palaeomeryx,* bearing branching ossicones. This situation persisted until Roman and Viret (1934) suggested that the two genera were synonymous; this suggestion was supported by Teilhard de Chardin (1939). De Chardin also suggested that a separate family should be created to accommodate *Lagomeryx, Procervulus* and 'other so called cervids'. This was left to Pilgrim (1941) who proposed the name Lagomerycidae for a family including the two genera named by de Chardin and *Climacoceras* which had been placed in the Cervidae (MacInnes 1936).

Stirton (1944) discusses the relationships of the palaeomerycids and states that *Lagomeryx* and *Palaeomeryx* are synonymous; he also proposes the retention of the family name Palaeomerycidae expanded to include:

> '. . . the Old World and New World non-antlered but horned and some hornless cervoids. The genera with forked horns from the Old World are included in the subfamily Palaeomerycinae and those from North America with pointed, bulbous or flat tipped horns are assigned to the Dromomerycinae.' (Stirton 1944).

Whitworth (1958) discusses the affinities of the palaeomerycids at some length, supporting the synonymy of *Lagomeryx* and *Palaeomeryx* and indicating the close affinity of palaeomerycids and cervids. This is contested by Ginsburg and Heintz (1966) who challenge the synonymy of *Lagomeryx* and *Palaeomeryx* and in their discussion of the genus *Palaeomeryx* they state:

> 'En dehors d'Europe, le genre a été signalé par Teilhard de Chardin (1939) dans le Miocène de Chine et par T. Whitworth (1958) dans le Miocène d'Afrique orientale. Dans les deux cas, on peut affirmer qu'il ne s'agit pas de Palaeomeryx ne serait-ce que par la présence, chez deux formes, d'une P_1.'

The presence of a P_1 in *Palaeomeryx africanus* is questioned by Gentry (1970) but a P_1 was certainly present in the species described by de Chardin (1939); which must therefore be removed from the genus *Palaeomeryx* and should revert to its previously applied name of *Lagomeryx simpsoni;* however the name *Lagomeryx* is not applicable as it was established (Roger 1904) to refer to European species which have been synonymized with *Palaeomeryx:* in this situation the species reverts to its original name—*Heterocemas simpsoni* Young 1937.

Pilgrim (1941) and de Chardin (1939) indicate close giraffoid affinities for the Palaeomerycidae (Lagomerycidae) and their evidence for this was summarized by Whitworth (1958):

> '(i) the unequal development of anterior and posterior external ribs on the upper molars; (ii) the characteristically corrugated enamel of the teeth; (iii) the occurrence of a permanent velvet over the bony parts of the "antlers".'

Whitworth objected to the first on the grounds that variation occurs in the strength of the ribs in both giraffids and cervids and he states:

> 'In fact, an unequal development of the anterior and posterior external ribs are found, to a varied degree in most cervids and giraffids alike; although generally speaking, the anterior rib is more angular and better defined in the deer than in the Giraffidae.' (Whitworth 1958).

This objection is valid as is his objection to the second piece of evidence on the basis of the great variability of the enamel in the molars of the giraffids and cervids. The third piece of evidence is the strongest and Whitworth's grounds for rejecting it are correspondingly weak, he states:

> 'Finally to regard the possession of non-deciduous, velvet covered "antlers" as diagnostic of early Giraffoidea is contrary to Pilgrim's own repeated opinion (1941 and 1947) that this was as likely to be the primitive cervoid condition as the giraffoid.' (Whitworth 1958).

This distinction is probably basic to the classification of the giraffids, cervids and palaeomerycids and Pilgrim's statement is given here:

> '. . . the skin covered "horn" was the most primitive and the nearest approximation to it is to be seen in the Lagomerycid and Giraffid "horn". From this original type it is easy to surmise that the deciduous antlered horn of the Cervidae arose, though the intermediate stage is as yet unknown.' (Pilgrim 1941).

Whitworth indicated that this could just as easily mean that the palaeomerycids were primitive cervids as giraffids but the ossicones are positive evidence in favour of the affinity of the palaeomerycids and giraffoids, whereas they can only be regarded as evidence for the affinity of palaeomerycids and cervids on purely hypothetical grounds. In this context Ginsburg and Heintz (1966) state:

> 'Les ossicones de *Palaeomeryx* offrent, avec ceux des Girafes, de si fortes similitudes que nous nous demandons s'il ne s'agit déjà d'un Girafide vrai.'

The upper dentition of *Zarafa* agrees with that of *Palaeomeryx* in many features but it also agrees with *Palaeotragus* and the skull shows close affinities with the palaeotragines. Unfortunately the skull of *Palaeomeryx* is not known but the presence of a dentition with some palaeomerycid features on a skull with giraffid affinities indicates the closeness of the palaeomerycids and the giraffids.

Much of the confusion over the affinities of the palaeomerycids can be attributed to the poorly defined limits of the family. Ginsburg and Heintz (1966) have removed *Walangania africanus* and *Heterocemas simpsoni* from the genus *Palaeomeryx* which limits the genus mainly to the Lower and Middle Miocene of Europe. They also suggested the removal of the Oligocene genera which lack ossicones, from the Palaeomerycidae, transferring them to a position as the common stock from which the giraffids and cervids evolved; this group was named the Dremotheriidae by Ginsburg and Heintz but it is of the same status as the other main groups and should therefore have superfamily status. This regrouping of the early ruminants results in an arrangement as shown (text fig. 12).

The North American members of the Palaeomerycidae were discussed in detail by Stirton (1944) who assigned them to the subfamily Dromomerycinae and indicated an origin for this group which was close to the origin of the cervids and palaeomerycines. Simpson (1945) treated the Dromomerycinae as a subfamily of the cervidae; while Crusafont (1952) placed the tribe Blastomerycini in the Palaeomerycinae and transferred the Dromomerycinae to the Giraffoidea. Ginsburg and Heintz (1966) proposed the inclusion of the blastomerycines in the Dremotheriidae. The blastomerycines are small, hornless pecorans, at the same level of evolution as the

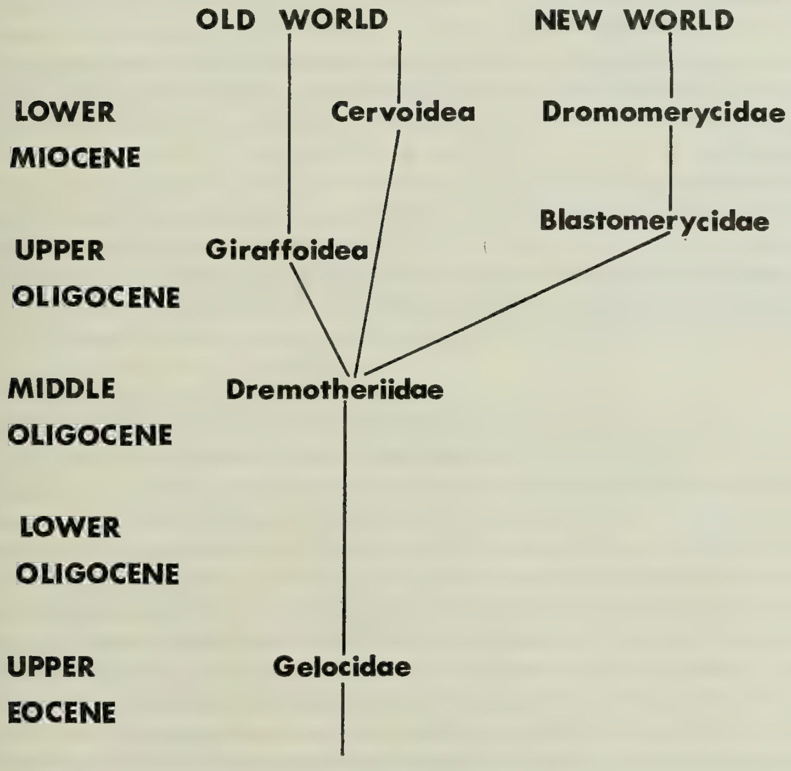
OLD WORLD
NEW WORLD
LOWER MIOCENE
Cervoidea
Dromomerycidae
Blastomerycidae
UPPER OLIGOCENE
Giraffoidea
MIDDLE OLIGOCENE
Dremotheriidae
LOWER OLIGOCENE
UPPER EOCENE
Gelocidae

FIG. 12. The interrelationships of the early, non-bovid ruminants.

dremotheriids and, with the exception of *Eumeryx*, they are an entirely New World group. At this level of pecoran evolution the forms are so similar that division into groups is difficult and it is proposed that the Dremotheriidae and Blastomerycidae should be treated as separate families of the Dremotherioidea. The Dromomerycidae probably originated from the Blastomerycidae.

Eumeryx culminis from the Hsanda Gol Formation was identified (Matthew and Granger 1924) as a blastomerycine and was so classified by Simpson (1945), it is the only blastomerycine from the Old World and is of Lower Oligocene age whereas the other blastomerycines are of Lower Miocene age. Stirton (1944) briefly discussed the position of *Eumeryx* and he states:

> 'As to whether *Eumeryx* is placed in the Cervoidea or Traguloidea is more or less arbitary but recognition of its pre-cervoid characters is quite important.' (Stirton 1944).

In view of the great difference of distribution in space and time and the difficulty of establishing relationships purely on the dentition, at this level of ruminant evolution; the affinity of *Eumeryx* with the other blastomerycines is doubtful.

The Pecora probably originated from the Traguloidea during the Upper Eocene or Lower Oligocene and of the two traguloid families the Gelocidae are the most likely to have given rise to the Pecora. In the gelocids true selenodonty is developed from more bunodont forms; thus *Lophiomeryx* has very bunoid lower molars showing few signs of true selenodonty while *Bachitherium* and *Prodremotherium* have molars which are very similar to those of *Dremotherium*. A detailed study of this group is needed and it is here that the divergence of the Bovoidea and other higher ruminants probably occurred.

The system shown (text fig. 12) appears more natural than any yet proposed for the evolution of the early, non-bovid ruminants. The members of the Dremotherioidea appear to form a natural unit and *Palaeomeryx* with its closely allied genera are included in the Giraffoidea. The whole pecoran classification at this level is in a state of flux as it relies upon very small differences and only the discovery of more localities and more complete material can resolve some of the outstanding problems.

IV. THE EFFECT OF THE OSSICONES ON GIRAFFOID EVOLUTION

With the exception of size, the most important differences between *Zarafa* and *Prolibytherium* are related to the frontal bones, ossicones and occipital region. The ossicones of *Zarafa* were developed supraorbitally and probably projected dorsolaterally as in *Samotherium sinense* (Bohlin 1926 pl. VI.). Each ossicone was probably a simple, conical projection about the same size as in *Okapia*. The ossicones of *Prolibytherium* are well known (pl. 7). If the origin of the giraffoids lies in the middle or late Oligocene then the divergent trends in the development of the ossicones must have been established very early to allow such great differences to evolve by the early Miocene; these trends may be revealed by the ossicones.

Frontal appendages are developed in the ruminants primarily for intraspecific combat and certain rules may be applied to their development; these were formulated by Geist (1965). Fighting in *Giraffa* (Innis 1958) and *Okapia* (Walther 1960 and 1962) consists of lateral display and the delivery of heavy blows to the sides and neck of the opponent with the head used as a club. Lateral display is the most primitive combat method used in the ruminants and is also found in the tylopods. With this combat method strong crushing or bending forces are not experienced along the length of the neck and therefore any tendency to increase the length of the neck is not inhibited by behavioural factors; indeed increase in length of the neck may confer a small selective advantage in combat as the length of the swing and therefore the force of the blow will be increased. This slight advantage would reinforce advantages resulting from other aspects of the animals behaviour such as feeding habits. With this combat method the force of blows delivered is on the lateral region of the frontals and therefore if a protuberance is developed it will be primitively in the supraorbital position; also head to head contact will not usually occur and a skin covered appendage will be effective and will retain its skin covering at least over most of its surface as in *Giraffa* or *Okapia*. Apart from the extant giraffids many of the palaeotragines and giraffines were long necked relatively slender animals, with small ossicones and it is likely that lateral combat methods were practised by all of them.

In *Prolibytherium* the ossicones consist of a solid outer layer of bone and a cancellous interior; frontal sinuses are not present. The derivation of the ossicones in *Prolibytherium* cannot be established but certain features of the skull may indicate their mode of origin. The anterior palmation projects antero-laterally from the supraorbital region and it is possible that the anterior region was derived from a supraorbital tine similar to that of *Zarafa*. At the posterior end of the ossicones the presence of paired pillars (pl. 10, fig. 2) suggests the derivation of this region from paired supraoccipital ossicones. The occurrence of supraorbital and parietal ossicones in other sivatheriids and palaeotragines indicates that giraffoids have the ability to develop ossicones in both regions.

The ossicones of *Prolibytherium* are the earliest advanced frontal appendages known in the ruminants. Geist (1965) relates the evolution of large frontal appendages to intraspecific combat involving frontal or head to head attack with wrestling and pushing between the heads. Geist states:

> '. . . cervid antlers should be regarded primarily as structures binding opponents together during pushing and wrestling matches.'

Thus the ossicones of *Prolibytherium* present a stage of evolution which is more advanced than that of *Zarafa*. The ossicones would also function in threat postures with reference to which Coope (1968) states:

> 'I believe that initially the "pedicels" evolved as threat display structures increasing the apparent surface area of the face and thus its deterrent value.'

Geist and Coope agree that the frontal appendages function in frontal display and attack when they are large and the effectiveness of the ossicones of *Prolibytherium* in increasing the apparent surface area of the face cannot be questioned.

Morphological and functional differences between the ossicones of *Zarafa* and *Prolibytherium* may suggest reasons for the divergence between the two main lines of giraffoid evolution. The selective advantage in intraspecific combat conferred by the large ossicones of the sivatheriids was a strong evolutionary force maintaining the large ossicones and also the short neck and limbs necessary for their effective use. The more primitive combat methods of the palaeotragines and giraffines tended to increase the selective advantage of a long neck and, more important, made possible the elongation of the neck under other selective forces.

V. A CLASSIFICATION OF THE GIRAFFOIDEA

The discovery of *Prolibytherium* and *Zarafa* in the Burdigalian of North Africa indicates that the origin of the giraffoids must lie in the late Oligocene and that divergence within the group occurred at this time. This was also stated by Ginsburg and Heintz (1966):

> 'On peut se demander si les soi-distant Cervides sans bois de la fin de l'Oligocene (*Amphitragulus*, *Dremotherium*, Blastomerycines) ne representant pas, non des Cervides primitifs, mais le stock commun d'ou sortiront a l'epoque suivant les Cervides, d'une part, et les Giraffoidea, d'autre part.'

Features of *Zarafa* and *Prolibytherium* indicate divergence very soon after their origin from the pregiraffoid stock and the establishment of a separate family to accommodate the sivatheres is proposed. The evolution of the giraffines and palaeotragines has followed similar trends and the divergence of these two groups probably did not occur until the middle Miocene, they are therefore retained as subfamilies within the family Giraffidae. This results in a classification of the Giraffoidea as summarized in text figure 13.

Superfamily **GIRAFFOIDEA** Simpson 1931

Family **PALAEOMERYCIDAE** Lydekker 1883

Canthumeryx New genus. L. Miocene; Africa.
Climacoceras MacInnes 1936. M–U. Miocene; Africa.
Heterocemas Young 1937. U. Miocene; Asia.
Palaeomeryx Von Meyer 1834. L. Miocene; Africa.
M–U. Miocene; Europe.
Procervulus Gaudry 1878. L–M. Miocene; Europe
Propalaeoryx Stromer 1926. L. Miocene; Africa.
Triceromeryx Villalta, Crusafont and Lavocat 1946.
L. Miocene; Europe.

Incertae sedis.
Progiraffa Pilgrim 1908. L. Miocene; Asia.

The Palaeomerycidae. At present the family is best regarded as a level of ruminant evolution equivalent to the primitive representatives of the Giraffidae and Sivatheriidae. This system was used quite drastically by Stirton (1944) who drew straight lines across his phylogenetic diagram to indicate levels of evolution and the limits of the family.

The genus *Triceromeryx* is placed in the Palaeomerycidae as it shows close similarities to the members of the genus *Palaeomeryx* from Sansan. The presence of a supraoccipital horn sets it apart from the other palaeomerycids and, owing to its strange nature, from all the sivatheriids and giraffids; however the material of *Triceromeryx* can be interpreted differently and it is possible that the supraoccipital ossicone does not belong to *Triceromeryx*, this is also suggested by Churcher (1970). The lower dentition of *Triceromeryx* is very palaeomerycine in form and each molar bears a strong '*Palaeomeryx* fold'. The P_4 is almost indistinguishable from a P_4 of *Palaeomeryx sansaniensis* (M.5409). The presence of a '*Palaeomeryx* fold' is not evidence of palaeomerycid affinities as such a fold is also present in some specimens of *Palaeotragus* and *Honanotherium* but in these genera the occurrence of the fold is irregular. The genus *Triceromeryx* is endemic to the Iberian peninsula and certainly does not effect the evolution of the advanced giraffoids.

The main problems relating to this family cannot be resolved until an exhaustive review of the European material is made. It is unlikely that the palaeomerycids gave rise to either of the other giraffoid families or to the cervids. They represent a Miocene expansion of the ruminants into an ecological niche which was later filled by the palaeotragines and cervids. Inter-relationships within the family are not known.

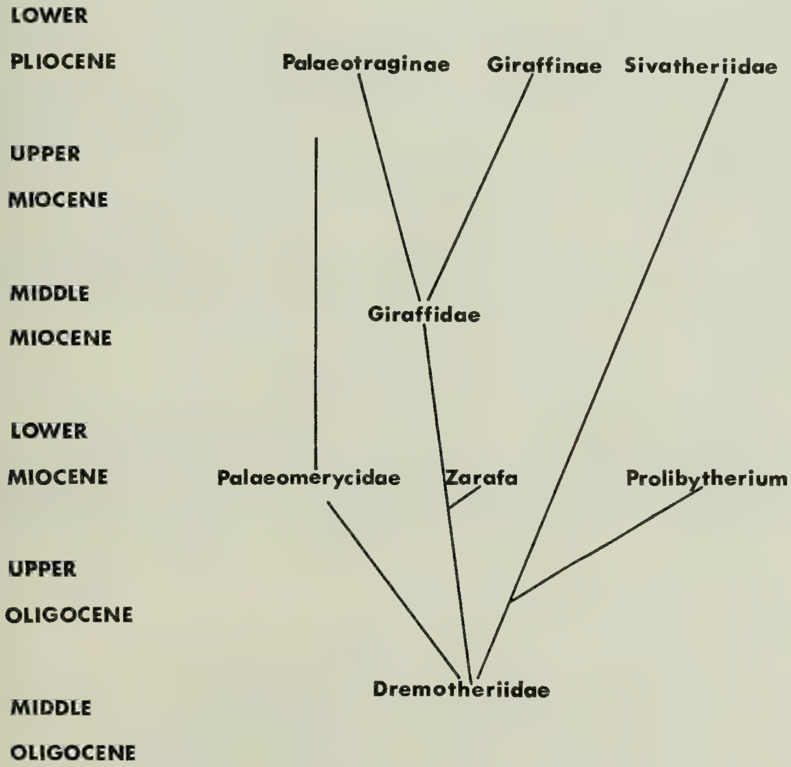
LOWER
PLIOCENE
UPPER
MIOCENE
MIDDLE
MIOCENE
LOWER
MIOCENE
UPPER
OLIGOCENE
MIDDLE
OLIGOCENE
Palaeotraginae
Giraffinae
Sivatheriidae
Giraffidae
Palaeomerycidae
Zarafa
Prolibytherium
Dremotheriidae

FIG. 13. The early evolution of the Giraffoidea.

Family *SIVATHERIIDAE* New family

Birgerbohlinia Crusafont 1952. L. Pliocene; Europe
Bramatherium Falconer 1845. M. Pliocene; Asia.
Helladotherium Gaudry 1860. L. Pliocene; Europe, Asia, and N. Africa.
Hydaspitherium Lydekker 1878. M. Pliocene; Asia.
Libytherium Pomel 1893. U. Pliocene and Pleistocene; Africa.
Prolibytherium Arambourg 1961. L. Miocene; Africa.
Sivatherium Falconer and Cautley 1835. U. Pliocene and Pleistocene; Asia.

SIVATHERIIDAE: *Prolibytherium* is the earliest representative of this family but even in this genus the ossicones are highly developed and the cheek teeth show hypsodont tendencies. The retention of a lacrymal fossa indicates the primitive nature of the genus. The family is characterized by its short neck and limbs, and also by the large ossicones; these are probably related features but they also indicate that members of the family fed near the ground and grazing forms may have developed. Meladze (1964) suggests that the family reached its climax in the late Miocene but I would place this climax in the Pliocene when the group was represented by fairly abundant, massively built forms throughout the Old World. The African genus *Libytherium* is probably the only Upper Pliocene and Pleistocene genus from Africa and with it may be synonymized such forms as *Griquatherium* Cooke and Wells 1947 and *Orangiotherium* van Hoepen 1932. The genus *Helladotherium* from Pikermi, is problematical as it lacks ossicones, indicating that it was probably the female form: with reference to this genus Matthew (1929) states:

> 'It appears not at all improbable that *Helladotherium* may be the female of *Bramatherium* or *Hydaspitherium*. The teeth are indistinguishable, and the skulls are by no means as diverse in degree, but differ in the same manner, as *Sivatherium* and "*Indratherium*" of the Upper Siwaliks.'

No further work has been done on this problem and *Helladotherium* is here included in the family as a valid genus, with the qualification that it is probably a female form.

Meladze (1964) also suggests that the sivatheriids were adapted to life in the savannahs but I suggest that they were probably woodland or forest forms, feeding on low vegetation or grasses of the woodland floor. The family was very successful and it may have survived in Asia to sub-recent times as suggested by Colbert (1936).

Family **GIRAFFIDAE** Gray 1821

Subfamily **PALAEOTRAGINAE** Pilgrim 1911

Giraffokeryx Pilgrim 1910. L. Pliocene; Asia.
Okapia Lankester 1901. Pleistocene and Recent; Africa.
Palaeotragus Gaudry 1861. U. Miocene; Europe, Asia, and Africa. L. Pliocene; Europe and Asia.

Samotherium Major 1888. U. Miocene; Africa. L. Pliocene
Europe and Asia.
Zarafa New genus. L. Miocene; Africa.

Subfamily. **GIRAFFINAE** Zittel 1893.

Bohlinia Matthew 1929. L. Pliocene; Europe.
Decennatherium Crusafont 1949. L. Pliocene; Europe.
Giraffa Brisson 1756. Pliocene; Europe and Asia.
Pleistocene; Asia and Africa.
Recent; Africa.
Honanotherium Bohlin 1926. Pliocene; Asia.

GIRAFFIDAE: A group of late Oligocene origin with *Zarafa* as the earliest known genus. The family is characterized by a tendency to increase the length of the neck and limbs. The giraffids reached their climax in the early Pliocene when they were well represented throughout the Old World. It was probably during the middle Miocene or slightly earlier that the group divided into two subfamilies; the palaeotragines and giraffines.

The palaeotragines were in many ways very progressive and the development of a hypso-brachyodont dentition in later members of the genera *Palaeotragus* and *Samotherium* indicates that they probably fed upon fairly low vegetation with a high proportion of ground vegetation in their diet. In any case they were utilizing an intermediate zone between the bovids and giraffines and in times of scarcity it is this zone which the other two groups would utilize at the expense of the palaeotragines. The subfamily has one extant member, the okapi which has survived in a tropical forest environment.

The giraffines have been relatively successful since the Pliocene. The series *Honanotherium, Bohlinia, Giraffa* suggested by Bohlin (1935) seems to be a natural sequence and is probably the true relationship.

VI. EAST AFRICAN RUMINANTS

During this work reference has been made to the Miocene ruminants of East Africa which were described by Whitworth (1958). A brief review of these ruminants has been made as I disagree with some of Whitworth's identifications. These ruminants are treated as a separate section as they are nearly all previously described forms and all depend upon previously described material; also it was felt that their inclusion with the Libyan forms would confuse the description of a regionally defined ruminant group.

Superfamily **TRAGULOIDEA** Gill 1872

Family **TRAGULIDAE** Milne-Edwards 1864

Genus ***DORCATHERIUM*** Kaup 1833

The agreement between *Dorcatherium chappuisi* from Rusinga and Turkana (Arambourg 1933) is very close and there is no doubt that these specimens are from the same species. The other three species described by Whitworth (1958) are *D. pigotti*, *D. parvum* and *D. songhorensis;* these are distinguished on a size basis only and with reference to these species Whitworth states:

> 'Further collecting may show that *D. songhorensis* is synonymous with *D. parvum* or *D. pigotti*, but for the present it seems preferable to treat the Songhor material separately.' (Whitworth 1958).

I agree with Whitworth on this point, there are certainly two smaller species of *Dorcatherium* and as further collections have not been made it is not possible to synonymize *D. songhorensis* with either of these.

The genus *Dorcatherium* is the only traguloid genus previously identified from the Miocene of Africa but included in the material identified as *Palaeomeryx africanus* (Whitworth 1958) are a few lower molars which differ anatomically from the type specimen. These molars exhibit traguloid features and agree closely with the lower molars of *Gelocus*.

Superfamily **TRAGULOIDEA** Gill 1872

Family **GELOCIDAE** Schlosser 1886.

DIAGNOSIS: Traguloids in which true selenodonty is developed; strong cingula developed on the labial or lingual sides of the cheek teeth. Metapodials fused to form cannon bones and side toes reduced. Lower premolars very simple. P_1 reduced and peg-like, separated from P_2 by a short diastema (After Schlosser 1886).

Genus ***GELOCUS*** Aymard 1855

DIAGNOSIS: A medium sized gelocid in which the selenodonty is less advanced than in most members of the family. Metaconid rounded anteriorly but less so than in *Lophiomeryx*. Premolars very simple. (Mainly after Schlosser 1886).

Gelocus whitworthi sp. nov.

DIAGNOSIS: A medium sized species of *Gelocus* possessing a rounded metaconid on the lower molars; the median valley of the lower molars is very open lingually. Length of lower molar row about 33 mm.

SYNONYMY: One specimen of this species—K.Sgr.368.49—was described by Whitworth (1958) with *Palaeomeryx africanus*.

DERIVATION OF NAME: The species is named after Dr. T. Whitworth who produced the first definitive account of African Miocene ruminants.

HOLOTYPE: K.Sgr.365.1949—a left mandibular fragment with lightly worn M_2 and M_3. From Songhor, Nyanza Province, Kenya. All specimens of this species are the property of the National Museum, Kenya.

LOCALITY AND HORIZON: Specimens are from Songhor and Rusinga Island Kenya. Both sites are referred to the Miocene.

MATERIAL:

K.Sgr.265.1949	Holotype; a left mandibular fragment with lightly worn M_2 and M_3.
K.Sgr.368.1949	An isolated M_1 showing slightly heavier wear than the holotype.
K.Sgr.581.1949	An isolated right M_3 showing light wear.
K.Sgr.159.1949	An isolated right M_2 showing medium wear.
K.R.30	An isolated right M_3, showing medium wear.

DESCRIPTION: The lower molars are almost the same size as *Walangania africanus*. On the M_2 the metaconid is conical with an anterior crest curving antero-lingually to meet the mesostylid at the antero-lingual corner of the tooth; this results in the concavity of the antero-lingual face of the metaconid similar to *Gelocus communis* but differing greatly from *Walangania* in which the metaconid is selenodont. The postero-lingual face of the metaconid is rounded with a feeble metastylid but lacking a fold such as is present in *Dorcatherium*. In *Walangania* the metastylid lies lingual to the anterior end of the entoconid whereas in *Gelocus* it is closely joined to the metaconid and lies lingual to the posterior end of the metaconid; as a result the median valley is very open lingually (pl. 13, fig. 5). The entoconid is conical with a strong anterior crest. The posterior end of the entoconid is forked and the labial branch meets the postero-lingual end of the hypoconid while the lingual branch is produced postero-lingually. This results in a strong vertical groove on the posterior face of the cuspid (pl. 13, fig. 4); a similar groove is present in *Gelocus communis* in which the lingual branch meets the postero-lingual extension of the hypoconid and the labial wing joins this part of the hypoconid. No such groove is present in *Lophiomeryx*, *Bachytherium* or *Prodremotherium*.

The protoconid is crescentic and extends antero-lingually around the anterior end of the metaconid; causing the anterior fossette to open lingually (pl. 13, fig. 4) but not to the same extent as in *Lophiomeryx*. The posterior region of the protoconid extends lingually and joins the postero-labial face of the metaconid from which a wing is produced as in *Walangania* and *Palaeomeryx*; however in *Gelocus* this wing is much more anteriorly situated resulting in a shorter anterior fossette and a longer median valley region. The anterior wing of the entoconid also meets the protoconid in this region. The hypoconid is crescentic and lower than the protoconid. M_2 has strong anterior and posterior cingula.

The metaconid of M_3 is more feeble than on M_2 and the anterior crest is weaker. In *Lophiomeryx* the anterior end of the metaconid is extremely shortened and rounded while in *Gelocus* it bears a strong crest and is truly selenodont. The entoconid is more selenodont in M_3 than M_2, this is mainly due to the presence of a strong crest in the posterior region. This crest extends posteriorly and lies lingual to the postero-lingual end of the hypoconid (pl. 13, fig. 4). The posterior end of the entoconid is not forked as in the M_2; this region is similar to *Gelocus communis* but differs from *Lophiomeryx* in which the entoconid has only a feeble posterior crest.

The protoconid is crescentic and its antero-lingual extension is stronger than in the M_2; resulting in the posterior shift of the lingual opening of the anterior fossette in the M_3 relative to the M_2 (pl. 13, fig. 4). The hypoconid is similar to that of the M_2 but the posterior region is shorter in the M_3 as it joins the posterior extension of the hypoconid. The accessory column consists of a strong entostylid running postero-labially from the posterior end of the entoconid and fusing with the strong hypoconulid. The hypoconulid is crescentic and curves postero-labially from the face of the hypoconid (pl. 13, fig. 4). At its posterior end the hypoconulid turns antero-lingually and almost encircles the entostylid. M_3 has a strong anterior cingulum and both M_2 and M_3 have strong entostylids in the median valleys. M_3 also has a stylid at the labial end of the posterior valley.

Features of their anatomy warrant the specific but not generic separation of these specimens from other species of *Gelocus*. Their presence in East Africa is important as representatives of the family Gelocidae are previously unrecorded from Africa.

TABLE 12

The Lower Dentition of *Gelocus whitworthi*

	M_1		M_2		M_3	
	Length	Width	Length	Width	Length	Width
K.Sgr.365.1949	—	—	10·8 mm	6·7 mm	14·7 mm	6·9 mm
K.Sgr.368.1949	9·5 mm	5·9 mm	—	—	—	—
K.Sgr.581.1949	—	—	—	—	14·5 mm	6·8 mm
K.Sgr.159.1949	—	—	10·4 mm	6·7 mm	—	—
K.R.30	—	—	—	—	15·0 mm	6·8 mm

Family **PALAEOMERYCIDAE** Lydekker 1883

Genus ***PROPALAEORYX*** Stromer 1926

DIAGNOSIS: 'Pecora of medium size, with shallow mandible and rather brachyodont, selenodont lower cheek teeth, closed from P_2 to M_3; P_1 isolated by a very short diastema. Enamel wrinkled. Lower molars with very strong metastylid and entostylid; pronounced median rib on lingual surface of metaconid, similar rib on entoconid; accessory stylid in median, external valley developed to varying degree.' (Whitworth 1958).

TYPE SPECIES. *Propalaeoryx austroafricanus* Stromer 1926; from the Lower Miocene of South West Africa.

Propalaeoryx nyanzae Whitworth 1958

DIAGNOSIS: 'A species of *Propalaeoryx* with lower molar series (M_{1-3}) measuring about 45 mm in length. All lower molars have prominent accessory tubercle in the median, external valley. Teeth rather lower crowned than in type species, *P. austroafricanus*.' (Whitworth 1958).

HOLOTYPE: M.21368 (K.324.47) Figured Whitworth 1958, fig. 12. A fragment of left mandible with M_1 and M_2 showing slight wear.

HORIZON: From the Lower Hiwegi Beds, Rusinga Island. Lower Miocene.

MATERIAL:

M.21368	Holotype.
K.1263.51	Isolated left M_2.
K.614.49	Anterior region of right M_3.
K.774.52	Right mandibular fragment with M_2 and M_3.
K.780.52	Newly erupted left M_3.
K.193.51	Heavily worn left M^2.
K.Mt.21	Lightly worn right M^1.
K.X.	Left maxillary fragment with M^1 and M^2.
K.Mt.67.51	Fragment of left maxilla with P^4 and M^1. (Listed as *Palaeomeryx africanus* by Whitworth 1958; table X.).
K.246.59	Heavily worn left M^1.

DESCRIPTION: Whitworth (1958) described the lower dentition only and upper molars here identified as *Propalaeoryx nyanzae* agree with the lower molars in details such as size, brachyodonty, degree of rugosity, depth of fossettes and strength of labial ribs and styles. The lower dentition is redescribed as it agrees closely with *Canthumeryx.*

Lower dentition. The enamel of the molars is finely rugose. M_2 has a strong anterior cingulum as in *P. austroafricanus* and *Canthumeryx*; this cingulum has a serrated occlusal edge and appears to consist of a series of small tubercles. The molars exhibit the same degree of brachyodonty as in *Canthumeryx.* On the M_2 the posterior crest of the metaconid is flexed labially in the unworn state and this flexion is indicated on the wear trace until medium wear has occurred. The lingual rib of the metaconid is as strong as that of *Canthumeryx* but does not equal the strength of this rib in *Palaeomeryx furcatus* or *Palaeomeryx magnus* in which the rib has a strong posterior fold. The metastylid is strong and projects lingually but it is weaker than the metastylid of some palaeomerycids. The entoconid is shortened in the posterior region and the posterior fossette opens lingually. The protoconid is crescentic and joins the anterior end of the metaconid; this end of the molar is very pointed as in *Canthumeryx* (pl. 14, fig. 1). The hypoconid is crescentic and its anterior end meets the protoconid in the median valley. The posterior end of the hypoconid is very long and is produced lingually.

The M_3 is similar to the M_2 in the anterior region. The posterior region of the hypoconid is produced lingually and meets the face of the strong entostylid. The hypoconulid is crescentic and joins the hypoconid labially and the entostylid lingually thus enclosing a large enamel island (pl. 14, fig. 1).

Upper dentition. The molars are four rooted with the lingual and labial pairs of roots fused. The enamel is more rugose than in *Walangania* and M^1 has a strong anterior cingulum and a weaker posterior cingulum. The parastyle of M^1 is strong with a pronounced labial rib which forms the antero-labial corner of the tooth. The paracone is stout and less transversely flattened than that of *Walangania*; this is a primitive feature resembling the traguloid condition. The labial rib of the paracone is stronger than that of *Walangania* (pl. 14, fig. 2) and resembles closely that of *Palaeomeryx* in which the rib flexes slightly anteriorly. The mesostyle is similarly developed in *Propalaeoryx, Walangania* and *Palaeomeryx.* The metacone has a feeble labial rib and the metastyle is strongly developed (pl. 14, fig. 2). The protocone is similar to that of *Palaeomeryx*; it is crescentic with a few small wings at the postero-labial end; these project into the medial valley and the anterior fossette (pl. 14, fig. 2). The anterior fossette is much shallower than in *Walangania* but resembles that of *Palaeomeryx.* The metaconule is crescentic; from its posterior region two strong accessory crests project into the fossette; these are strongly developed in all the molars and an enamel island is formed early in wear, this island is large and shallow (pl. 14, fig. 2). As wear continues the first enamel island is lost and a smaller one is developed at the posterior end of the fossette. Accessory crests are very feeble when present in *Walangania.*

M^2 is similar to M^1 in all its main features. Each molar has a strong entostyle in the median valley and a very strong anterior cingulum which has a serrated edge as in the lower molars.

The P^4 is similar to that of *Palaeomeryx.* The labial region of the tooth is not known but the lingual region of the metacone is preserved. The protocone is crescentic and from its posterior region an extremely strong accessory crest divides the fossette into anterior and posterior regions (pl. 14, fig. 2); in the posterior region a series of small tubercles and folds are present on the face of the protocone and metacone. A strong cingulum forms a swelling at the base of the lingual face of the protocone (pl. 14, fig. 3) a similar though weaker cingulum is occasionally present in *Palaeomeryx* and *Walangania.*

The upper dentition with its shallow fossettes, stout labial cusps, strong styles and cingula and complications of the cusps by accessory crests or tubercles is more primitive than the dentition of *Palaeomeryx* or *Walangania* and in many features agrees closely with the tragulid dentition. The description of the upper molars of *Propalaeoryx* shows that though it is more primitive than *Palaeomeryx* it shows closer affinities with this type of dentition than with the primitive bovids.

The affinities of Propalaeoryx. Stromer (1926) indicated that *Propalaeoryx* was a member of the Bovidae but Arambourg (1933) states:

> '*Propalaeoryx austro-africanus* Stomer appartient à une espèce d'assez grande taille et possède d'incontestables traits de Cervidé primitif.'

Whitworth (1958) discusses the affinities of *Propalaeoryx* and states:

> 'Indeed in everything except size, the lower molars of *Propalaeoryx* are precisely like those of *Micromeryx* from the Miocene of Europe.'

In spite of evidence presented by dentition, Whitworth continues his argument, citing isolated ruminant limb bones which he tentatively identifies as *Propalaeoryx*; especially a single metatarsal which:

> '. . . exhibits a bovid condition in the housing of the extensor tendon while retaining a remarkably cervid-like development of the shaft.' (Whitworth 1958).

The reasons for this identification rest upon the fact that the bone agrees in size with *Propalaeoryx nyanzae;* however true bovid dentitions of a similar size have been found in these deposits. Whitworth considered this single bone to be sufficient to cast grave doubts on the supposed cervid affinities of the genus but I do not feel that this tentative evidence can outweigh positive evidence presented by the dentition in favour of palaemerycid affinities for *Propalaeoryx*. As stated the dentition of *Propalaeoryx* is similar to that of *Palaeomeryx* and the strong metastylid, which is much stronger than that of *Walangania,* is a palaeomerycid rather than a bovid character. The lower premolars of *Propalaeoryx austroafricanus* are virtually indistinguishable from those of some palaeomerycids or from *Canthumeryx*. For these reasons *Propalaeoryx* is classified as a member of the *Palaeomerycidae*.

It is possible that *Canthumeryx* and *Propalaeoryx* are representatives of a new group of ruminants which is of African origin but in the absence of more material I prefer to group them with an existing and certainly closely related family.

TABLE 13

The Dentition of *Propalaeoryx nyanzae*

Lower Dentition

	M_1		M_2		M_3	
	Length	Width	Length	Width	Length	Width
B.M.21368	13·6 mm	7·2 mm	13·7 mm	7·9 mm	—	—
K.614.49	—	—	—	—	—	8·4 mm
K.1263.51	—	—	12·5 mm	7·7 mm	—	—
K.774.52	—	—	13·5 mm	7·8 mm	19·0 mm	8·3 mm
K.780.52	—	—	—	—	19·6 mm	8·2 mm

Upper Dentition

	P^4		M^1		M^2	
	Length	Width	Length	Width	Length	Width
K.193.51	—	—	—	—	12·5 mm	13·1 mm
K.Mt.21	—	—	14·2 mm	14·4 mm	—	—
K.X.	—	—	13·0 mm	14·0 mm	12·0 mm	—
K.Mt.67.51	10·0 mm	11·5 mm	12·6 mm	13·1 mm	—	—
K.246.59	—	—	12·5 mm	14·0 mm	—	—

BOVIDAE Incertae Sedis

Genus ***WALANGANIA*** Whitworth 1958

DIAGNOSIS: Small, lightly constructed pecoran. Frontal appendages unknown. Mandible with prominent angle and large recurved coronoid process. Cheek teeth closed from P_2 to M_3. First premolar lost. Lower molars brachyodont, selenodont and narrow. Protoconid and hypoconid angular and compressed antero-posteriorly. Upper molars square, brachyodont and selenodont. Paracone with strong labial rib, metacone lacking labial rib. Enamel of cheek teeth finely rugose. Pelvis and rear limbs of advanced pecoran type. (After Whitworth 1958).

Walangania africanus (Whitworth) 1958

Palaeomeryx africanus Whitworth 1958.
Walangania gracilis Whitworth 1958.
Kenyameryx africanus Ginsburg and Heintz 1966.

DIAGNOSIS: As for genus.

REMARKS: The species *Palaeomeryx africanus* was established on the basis of a large number of upper and lower dentitions as well as a considerable amount of postcranial material. Ginsburg and Heintz (1966) removed the species from the genus *Palaeomeryx* on the basis of a supposed presence of a P_1 and the more primitive nature of the anterior premolars. The name *Kenyameryx* was suggested to accommodate the species. The presence of a P_1 was disputed by Gentry (1970) who identifies the P_1 as a second deciduous premolar.

The genus *Walangania* is known from the holotype only; this is an almost complete, associated skeleton in which the deciduous dentition and the first permanent molars are erupted. Except in the degree of wear the permanent molars are indistinguishable from those which Whitworth described as *Palaeomeryx africanus*. Although Whitworth states that the '*Palaeomeryx* fold' is absent in the holotype a fold is certainly present and is as strong as in many specimens of *Palaeomeryx africanus*. The dimensions of the teeth are also very similar in *Walangania* and *Palaeomeryx africanus* (table 14).

The main differences in the diagnoses of *Walangania gracilis* and *Palaeomeryx africanus* are the presence of a P_1 and a '*Palaeomeryx* fold' in *P. africanus* but neither of these differences are acceptable on closer investigation. The other differences between the species result mainly from the juvenile condition of the *Walangania* holotype and are insufficient to warrant the continued separation of the two species.

Palaeomeryx africanus was described earlier in the publication than *Walangania gracilis* but the generic name *Palaeomeryx* is not applicable to the material. The name *Kenyameryx* suggested by Ginsburg and Heintz (1966) cannot be used as the name *Walangania* has precedence. The trivial name 'africanus' is retained as it has page precedence over the trivial name 'gracilis'.

The affinities of Walangania africanus. The affinities of *Walangania gracilis* were discussed by Whitworth (1958) who concludes:

> 'For the present, *Walangania* must be regarded as a pecoran genus of doubtful systematic position, although the available evidence may slightly favour inclusion with the Cervidae.'

The affinities of *Palaeomeryx africanus* were implied by its generic name and therefore with the synonymy of *P. africanus* and *W. gracilis* the affinities of the species *Walangania africanus* should lie with the Palaeomerycidae; however a study of the material indicates that even this affinity is very doubtful.

The lower molars of *Walangania* exhibit weak lingual ribs and styles these agree in strength with those of *Eotragus* and are weaker than is usual in *Palaeomeryx*. The metaconid and entoconid are aligned almost parallel to the long axis of each lower molar in *Walangania* and *Eotragus* but in *Palaeomeryx* these cuspids usually have a diagonal orientation. The metaconids and entoconids of the lower molars

Table 14

The dentition of *Walangania africanus*
(Numbers 1 to 3 are listed by Whitworth 1958, as *Palaeomeryx africanus*.)
(Number 4 is listed as *Walangania gracilis*.)

Upper Dentition

	P4		M1		M2		M3	
	Length	Width	Length	Width	Length	Width	Length	Width
(1) K.Sgr.27.49	8·0 mm	8·6 mm	9·6 mm	9·3 mm	—	—	—	—
(2) K.694.47	7·7 mm	8·6 mm	10·5 mm	10·0 mm	11·5 mm	11·5 mm	11·5 mm	11·0 mm
(3) K.547.47	6·6 mm	8·7 mm	9·7 mm	9·0 mm	10·5 mm	10·5 mm	10·0 mm	9·8 mm
(4) B.M.21389	—	—	10·7 mm	10·1 mm	—	—	—	—
(5) *Eotragus sansaniensis* (From Thenius 1952)	8·5 mm	10·0 mm	10·0 mm	13·0 mm	12·0 mm	14·0 mm	13·0 mm	14·0 mm

Lower Dentition

	M_1		M_2	
	Length	Width	Length	Width
(1) K.Sgr.48.47	11·0 mm	6·3 mm	12·0 mm	7·0 mm
(2) B.M.21358 (Holotype)	11·5 mm	6·6 mm	12·0 mm	7·2 mm
(3) B.M.21359	11·5 mm	6·4 mm	—	—
(4) B.M.21388	11·0 mm	6·0 mm	—	7·0 mm
(5) *Eotragus sansaniensis* (From Thenius 1952)	10·4 mm	7·0 mm	11·3 mm	8·2 mm

tend to be more selenodont in *Walangania* and *Eotragus* than in *Palaeomeryx*. The labial ribs and styles of the upper molars are far weaker in *Walangania* and *Eotragus* than in *Palaeomeryx*. In all these features *Walangania* and *Eotragus* agree and each differs from *Palaeomeryx*, the main feature in which *Palaeomeryx* and *Walangania* agree is the presence of a '*Palaeomeryx* fold' on the lower molars of both genera; such a fold is unknown in the bovids but occurs in most other primitive ruminants, its presence in *Walangania* is insufficient to debar this genus from affinity with the bovids.

Gentry (1970) has also suggested bovid affinities for *Walangania* on the basis of its mandibular ramus and he states:

> 'It also has a moderately deep ramus, so it is quite possible that it will one day be shown to be a bovid.'

The distinction between bovoids, giraffoids and cervoids is very difficult in species of Burdigalian age but the dentition of *Walangania* exhibits features which indicate affinity with early bovids and for this reason it is here treated as a bovid; however all the features used exhibit variation and the tentative nature of these interpretations must be emphasized.

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PLATE 1

Fig. 1. ***Dorcatherium libiensis*** sp. nov. Right mandible, occlusal aspect. Holotype (M.26684) ×1·6 approx.

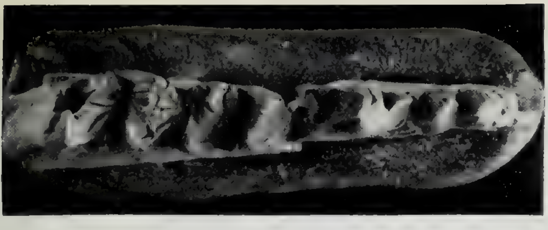
Fig. 2. ***Canthumeryx sirtensis*** gen. et. sp. nov. Right M_1 and D_4; occlusal aspect. (M.26683) ×1·6 approx.

Fig. 3. ***Canthumeryx sirtensis*** gen. et sp. nov. Right M_1; lingual aspect. (M.26683) ×1·4 approx.

Fig. 4. ***Canthumeryx sirtensis*** gen. et sp. nov. Right mandible; occlusal aspect. Holotype (M.26682).

Fig. 5. ***Canthumeryx sirtensis*** gen. et sp. nov. Right P_4 and P_3; occlusal aspect. (M. 26683) ×1·5 approx.

Fig. 6. Palaeomerycidae indet. Ossicones; anterior aspect. (M.26690).



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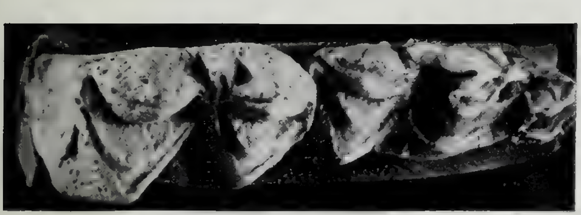

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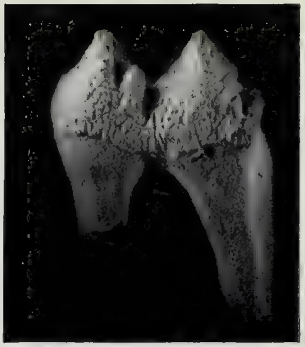

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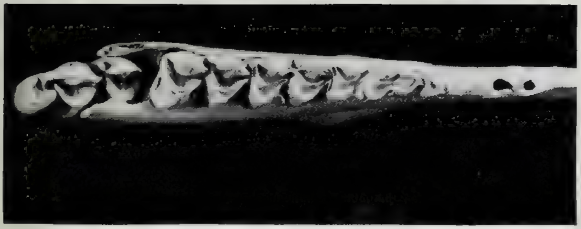

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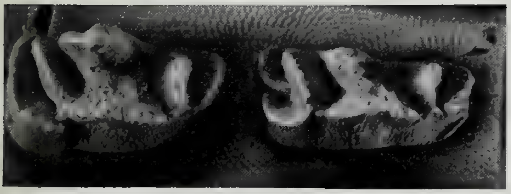

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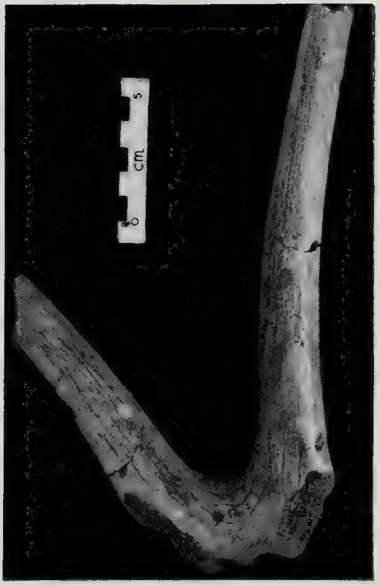

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PLATE 2

Zarafa zelteni gen. et sp. nov. Skull; lateral aspect. Holotype (M.26670).

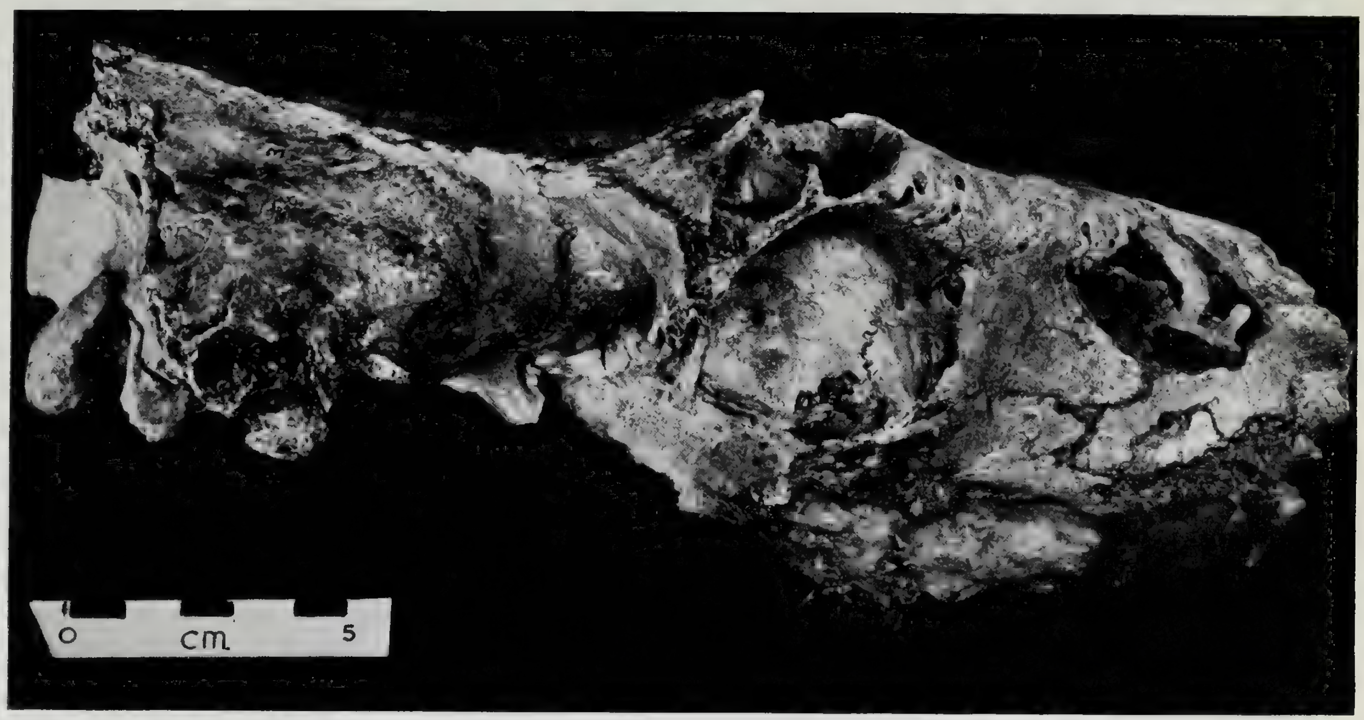
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PLATE 3

Zarafa zelteni gen. et sp. nov. Skull; dorsal aspect. Holotype (M.26670).

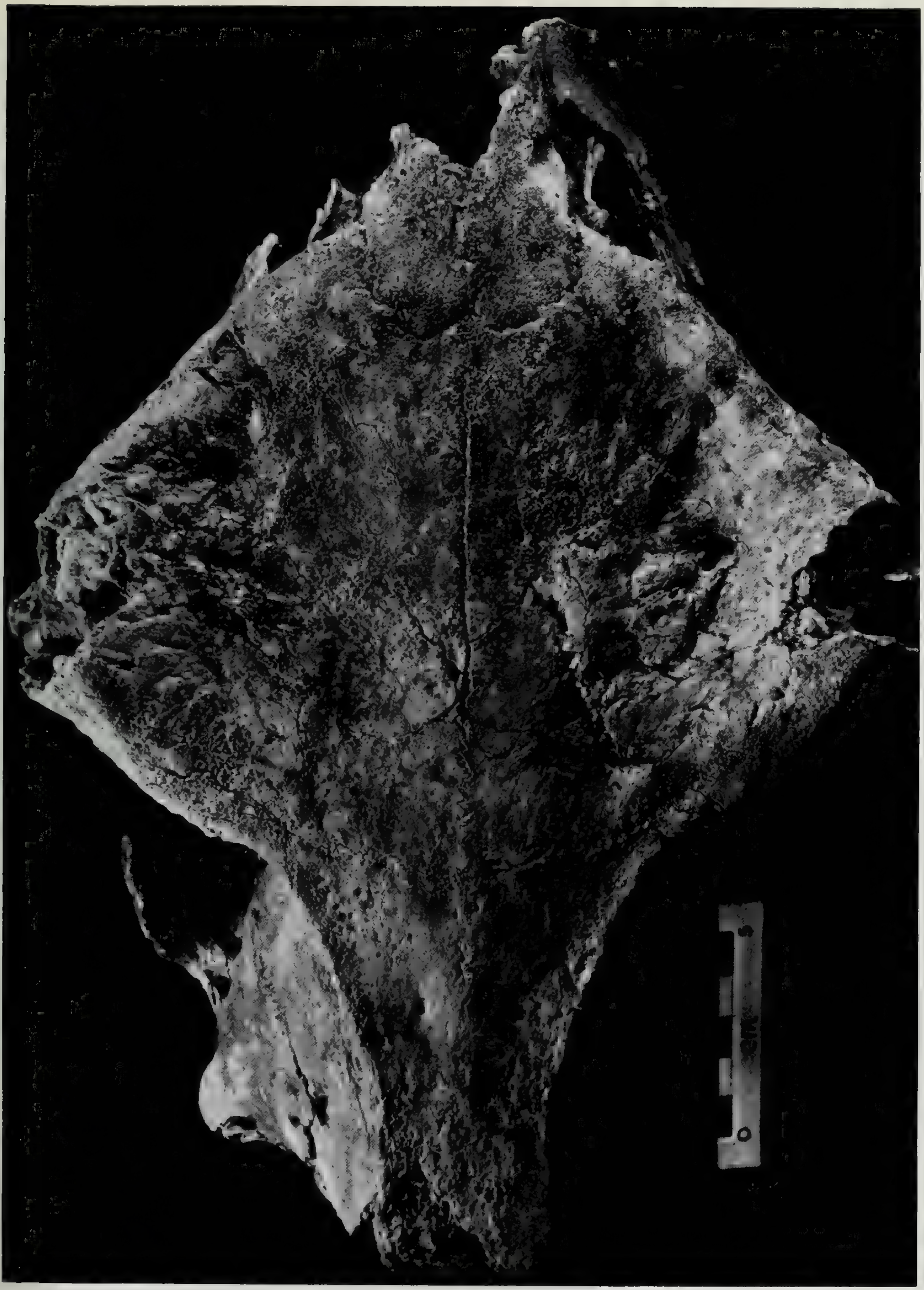
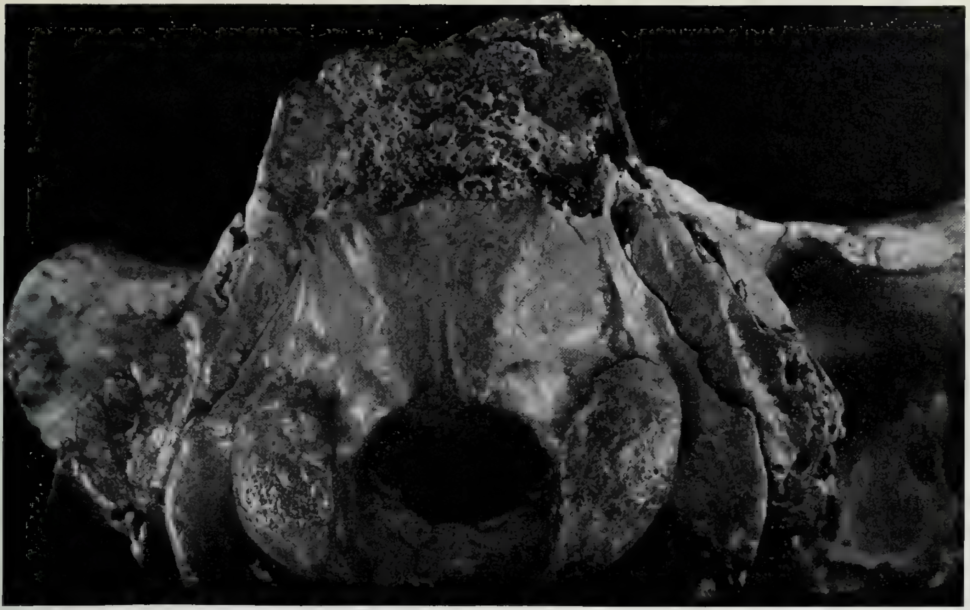


PLATE 4

FIG. 1. ***Zarafa zelteni*** gen. et sp. nov. Supraoccipital region; posterior aspect. Holotype (M.26670) × 1·2 approx.

FIG. 2. ***Zarafa zelteni*** gen. et sp. nov. Basicranial region; ventral aspect. Holotype (M.26670) × ·68 approx.

FIG. 3. ***Zarafa zelteni*** gen. et sp. nov. Right mandible; lingual aspect. (M.26675) × ·54 approx.



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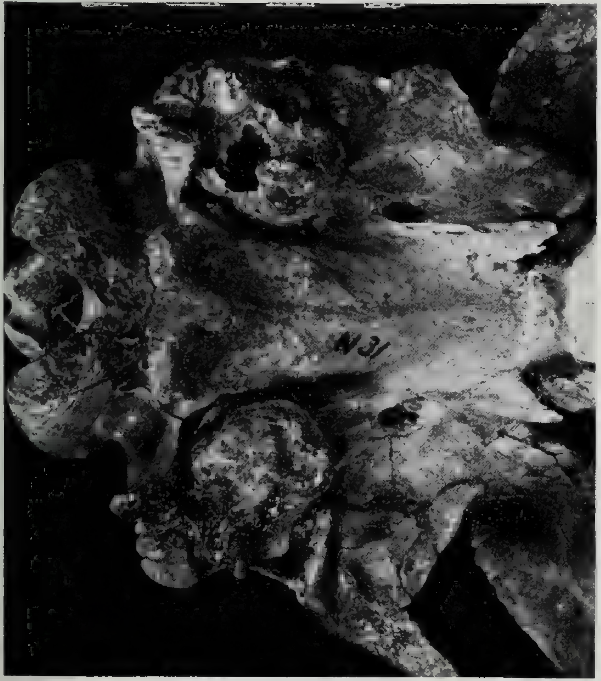

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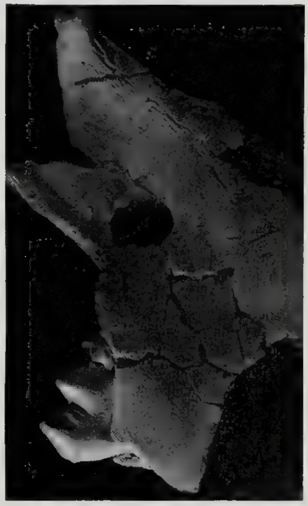

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PLATE 5

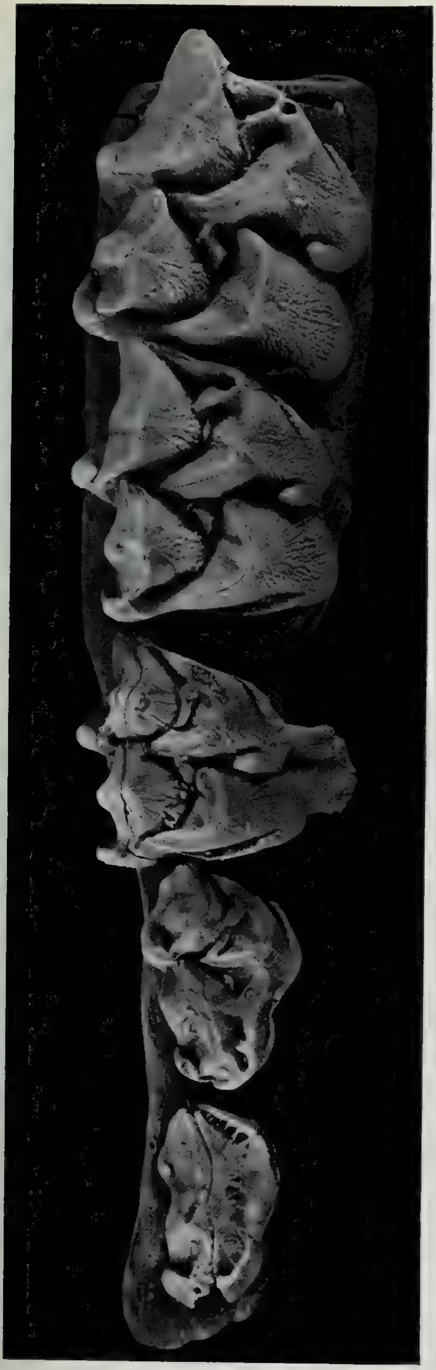
Fig. 1. ***Zarafa zelteni*** gen. et sp. nov. Left upper, juvenile dentition; occlusal aspect. (M.26672) × 1·7 approx.

Fig. 2. ***Zarafa zelteni*** gen. et sp. nov. Right M_2; occlusal aspect. (M.26677) × 1·3 approx.

Fig. 3. ***Zarafa zelteni*** gen. et sp. nov. Right M_2; lingual aspect. (M.26677) × 1·3 approx.

Fig. 4. ***Zarafa zelteni*** gen. et sp. nov. Right M_3; occlusal aspect. (M.26675) × 1.3 approx.

Fig. 5. ***Zarafa zelteni*** gen. et sp. nov. Right M_3; occlusal aspect. (M.26676) × 1·7 approx.



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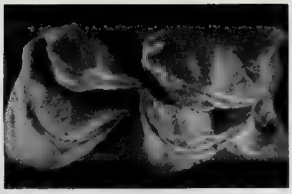

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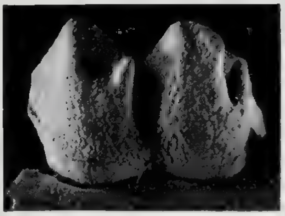

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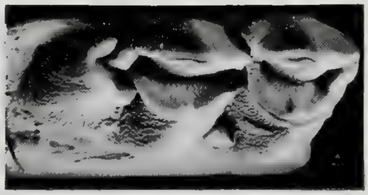

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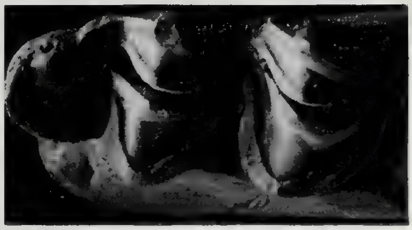

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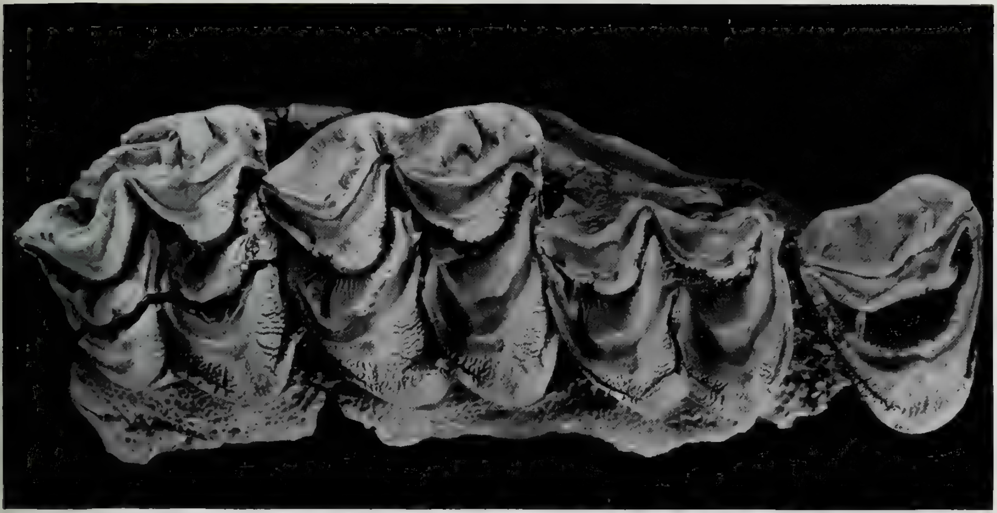
PLATE 6

FIG. 1. ***Zarafa zelteni*** gen. et sp. nov. Right upper dentition; occlusal aspect. (M.26671) ×1·7 approx.

FIG. 2. ***Zarafa zelteni*** gen. et sp. nov. Right upper dentition; labial aspect. (M.26671) ×1·7 approx.



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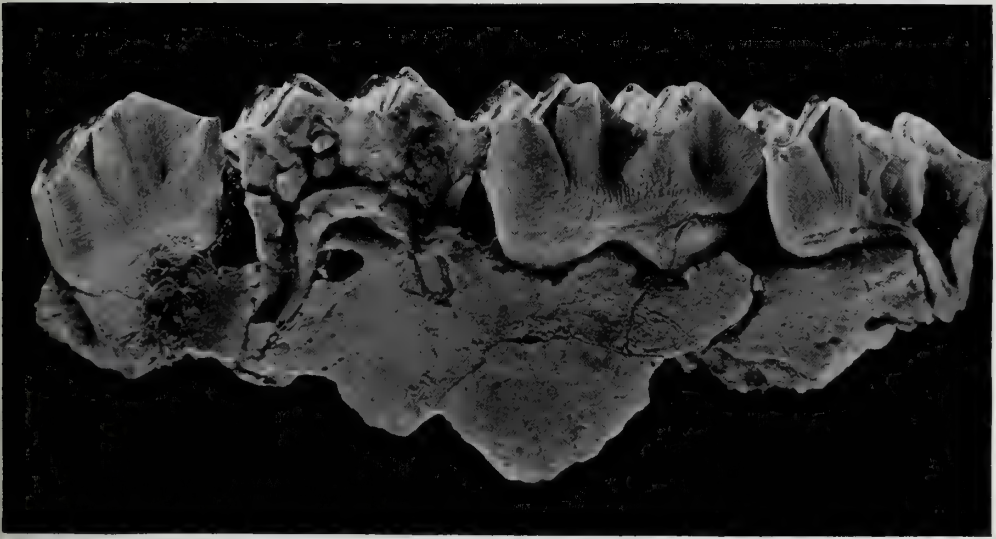

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PLATE 7

Prolibytherium magnieri Arambourg 1961. Skull and ossicones; ventral aspect. (M.21901).

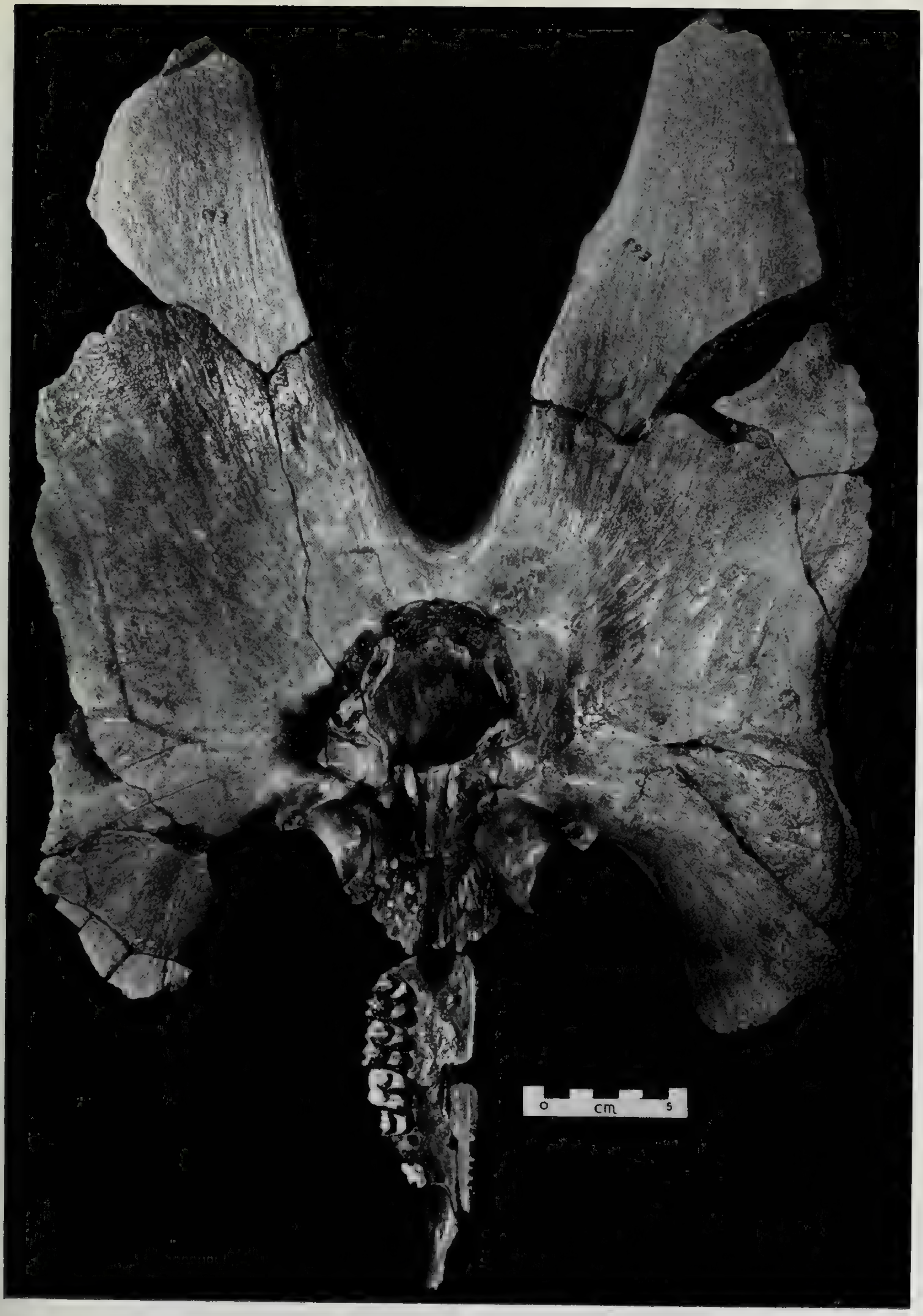
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PLATE 8

Prolibytherium magnieri Arambourg 1961. Left maxilla and upper dentition; lateral aspect. (M.21901) × 1·4 approx.

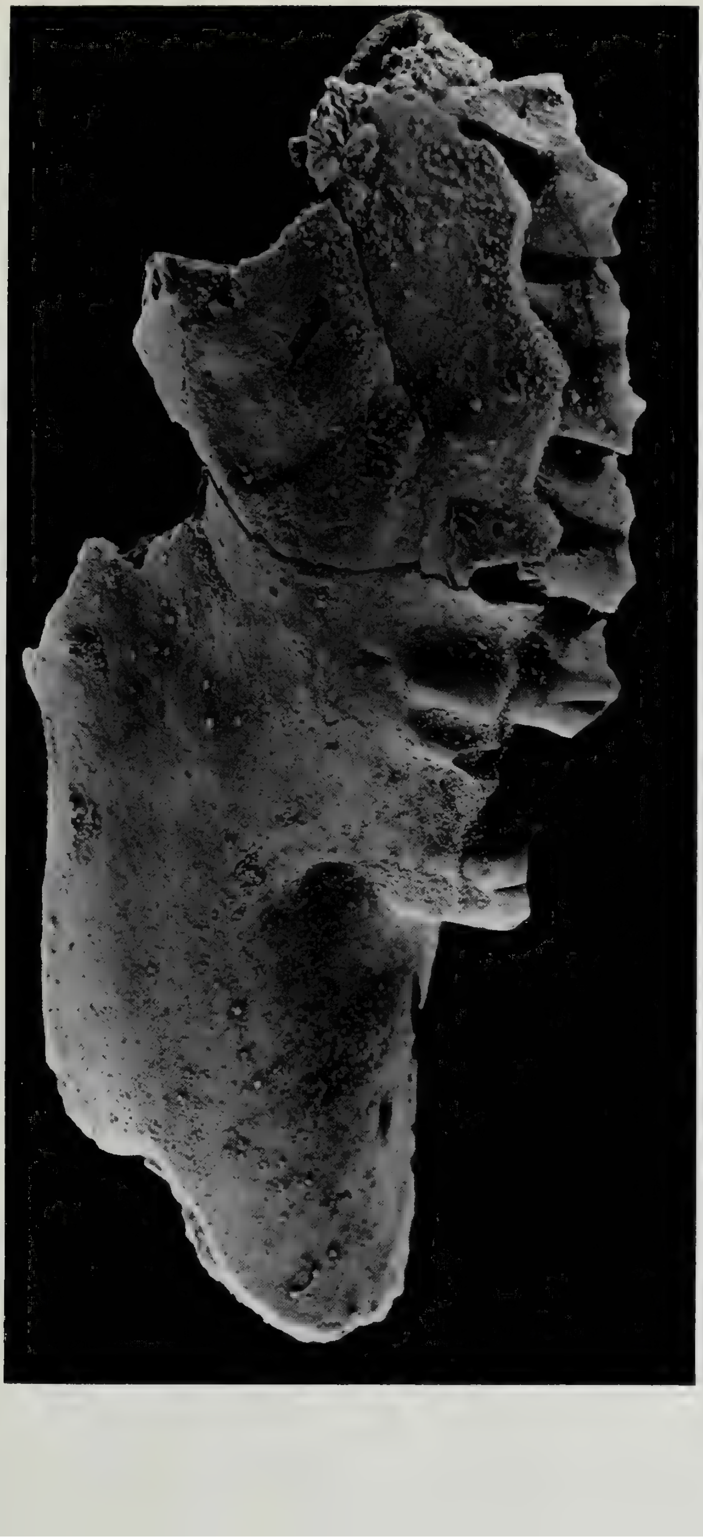


PLATE 9

Prolibytherium magnieri Arambourg 1961. Left upper dentition and palate. (M.21901) ×1·4 approx.

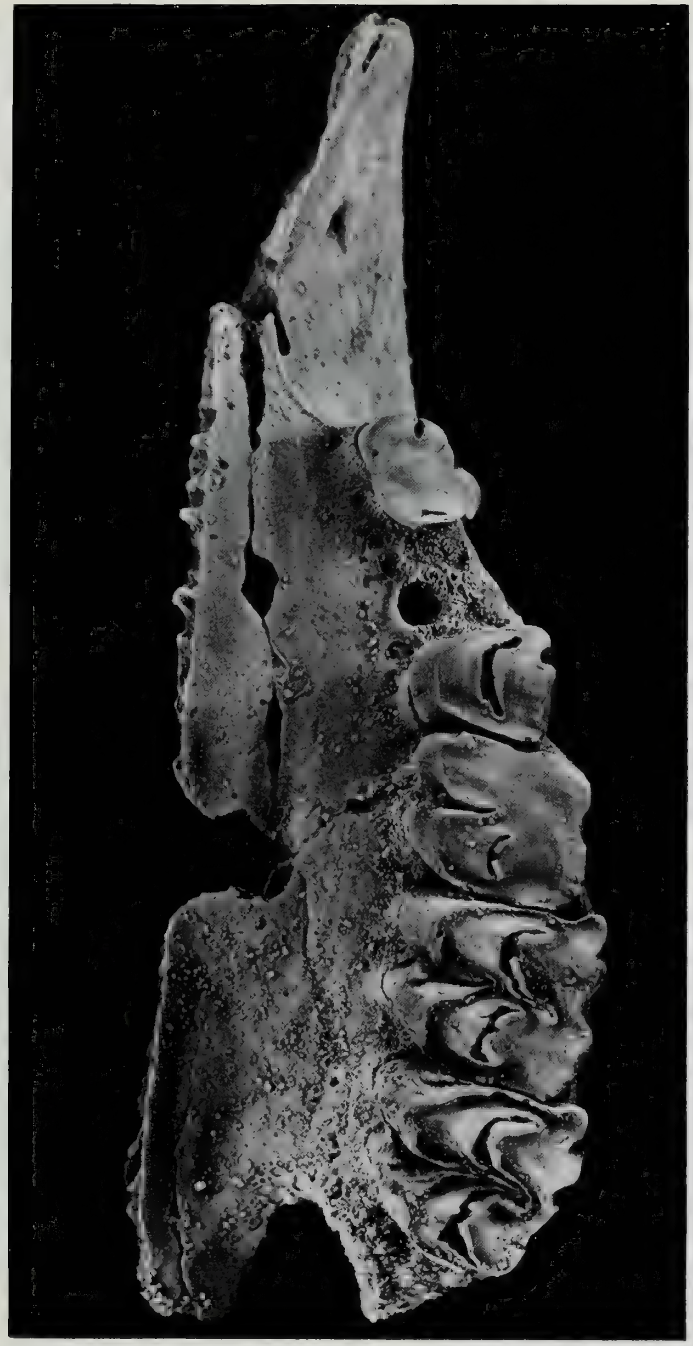


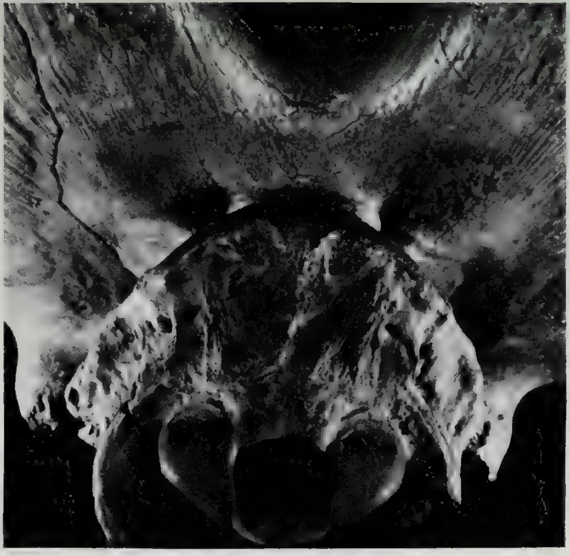
PLATE 10

FIG. 1. ***Prolibytherium magnieri*** Arambourg 1961. Basicranial region; ventral aspect. (M.21901) ×0·8 approx.

FIG. 2. ***Prolibytherium magnieri*** Arambourg 1961. Occipital region; posterior aspect. (M.21901) ×0·6 approx.

FIG. 3. ***Prolibytherium magnieri*** Arambourg 1961. Left M_3; occlusal aspect. (M.26681) ×2 approx.

FIG. 4. ***Prolibytherium magnieri*** Arambourg 1961. Left M_3; lingual aspect. (M.26681) ×2 approx.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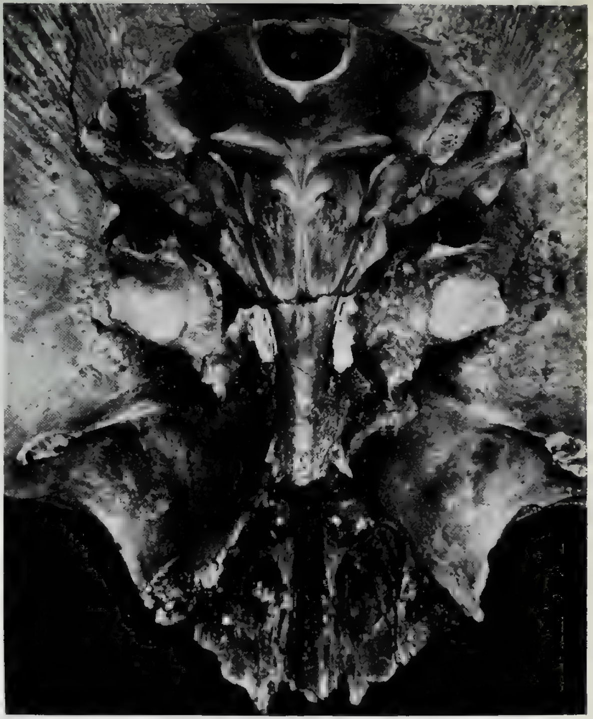
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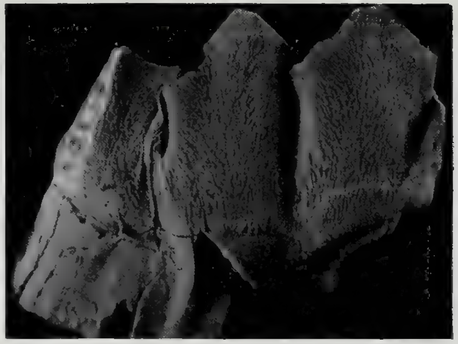
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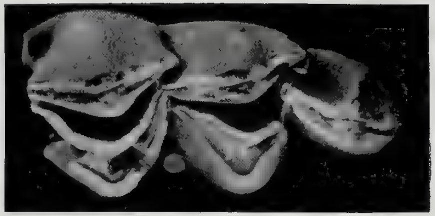
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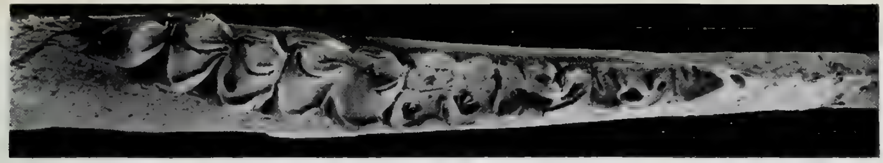
PLATE 11

FIG. 1. ***Prolibytherium magnieri*** Arambourg 1961. Right mandible; occlusal aspect. (M.21899) ×1 approx.

FIG. 2. ***Prolibytherium magnieri*** Arambourg 1961. Right mandible; labial aspect. (M.21899) ×1 approx.

FIG. 3. ***Prolibytherium magnieri*** Arambourg 1961. Right petrosal; ventro-lateral aspect. (M.21901) ×1·7 approx.

FIG. 4. ***Prolibytherium magnieri*** Arambourg 1961. Right petrosal; dorso-medial aspect. (M.21901) ×2 approx.



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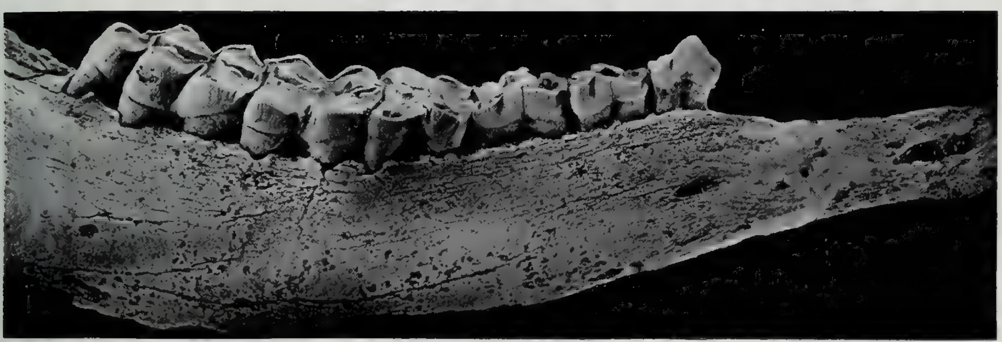

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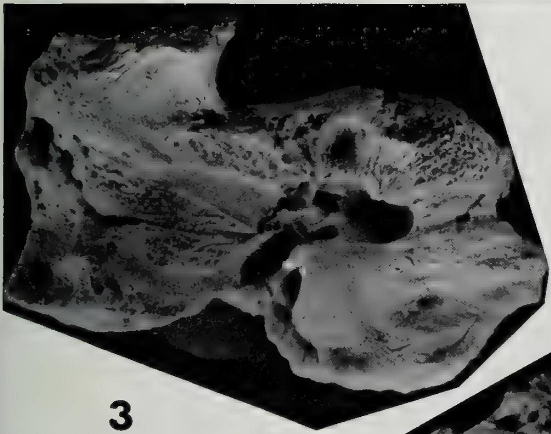

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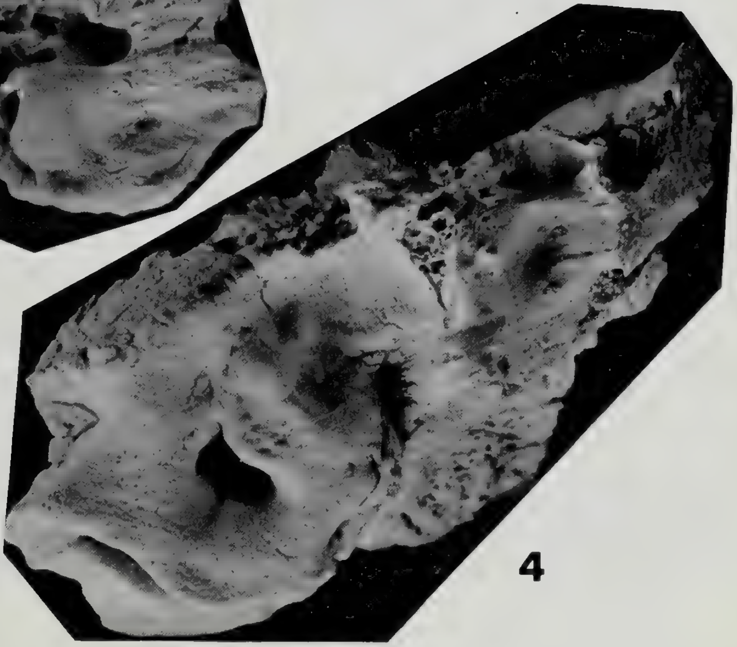

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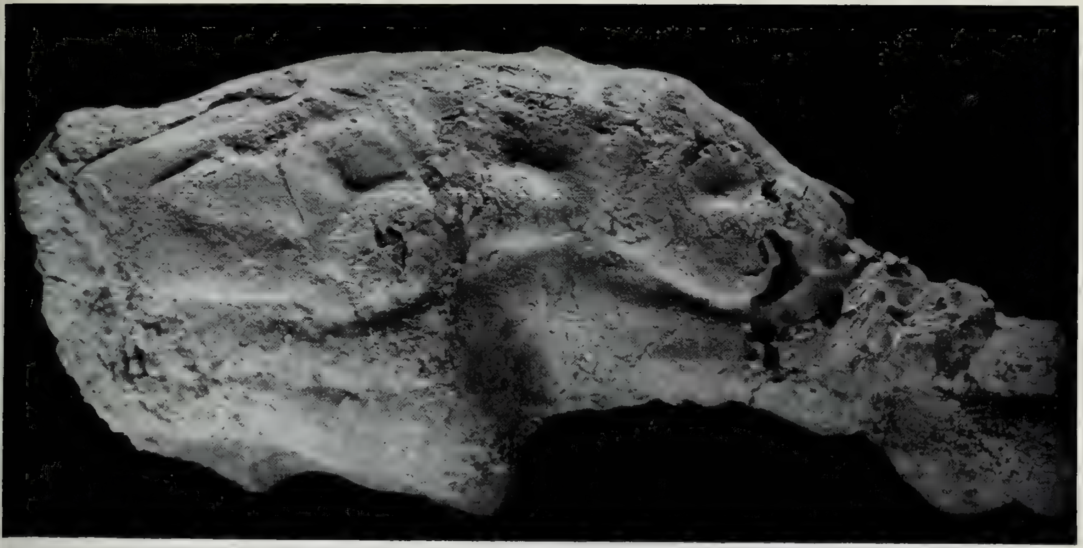
PLATE 12

FIG. 1. ***Prolibytherium magnieri*** Arambourg 1961. Endocranial cast; right lateral aspect. (M.26678) ×1·3 approx.

FIG. 2. ***Prolibytherium magnieri*** Arambourg 1961. Endocranial cast; dorsal aspect. (M.26678) ×1·3 approx.



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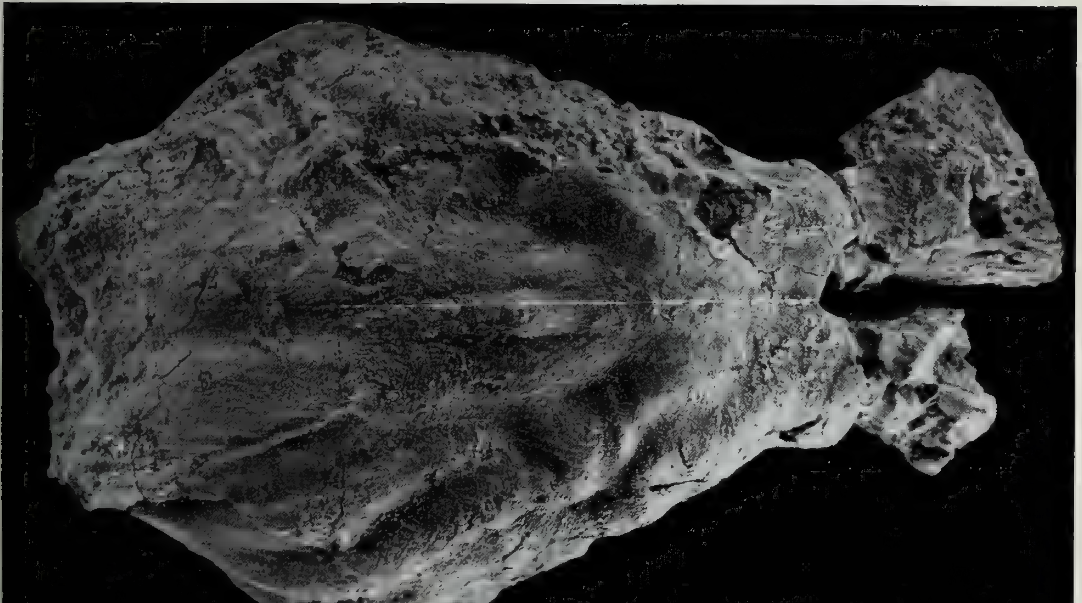

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PLATE 13

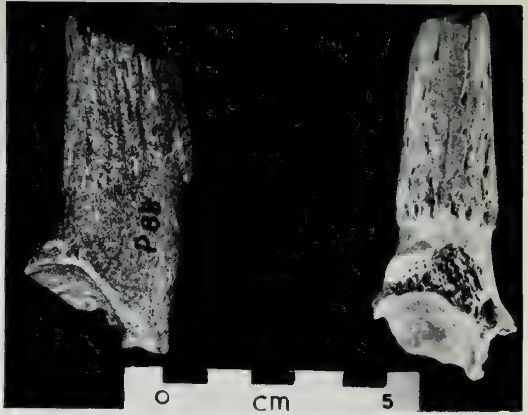
FIG. 1. Left. **Protragocerus** sp. Horncore; left lateral aspect. (M.26687). Right. **Eotragus** sp. Horncore; right lateral aspect. (M.26688).

FIG. 2. **Gazella** *sp.* Left mandible; occlusal aspect. (M.26685) ×0·78 approx.

FIG. 3. **Gazella** *sp.* Left mandible; lingual aspect. (M.26685) ×0·78 approx.

FIG. 4. **Gelocus whitworthi** sp. nov. Left M_2 and M_3; occlusal aspect. Holotype (K.Sgr. 365.1949) ×3·3 approx.

FIG. 5. **Gelocus whitworthi** sp. nov. Left M_2 and M_3; lingual aspect. Holotype (K.Sgr. 365.1949) ×3·3 approx.



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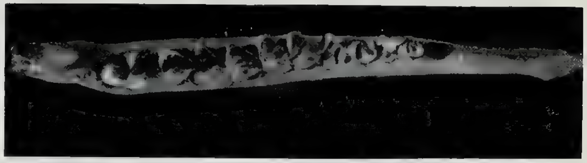

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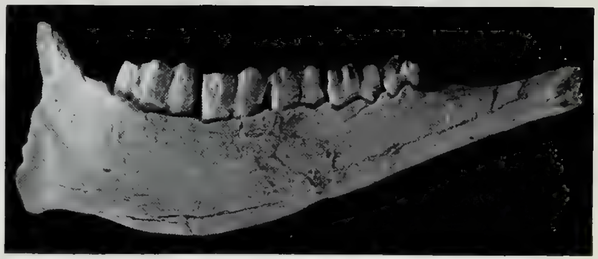

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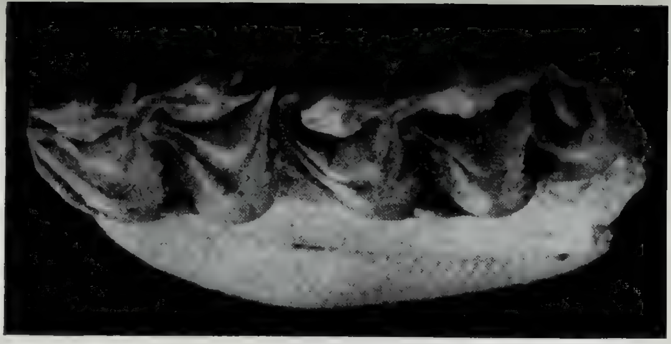

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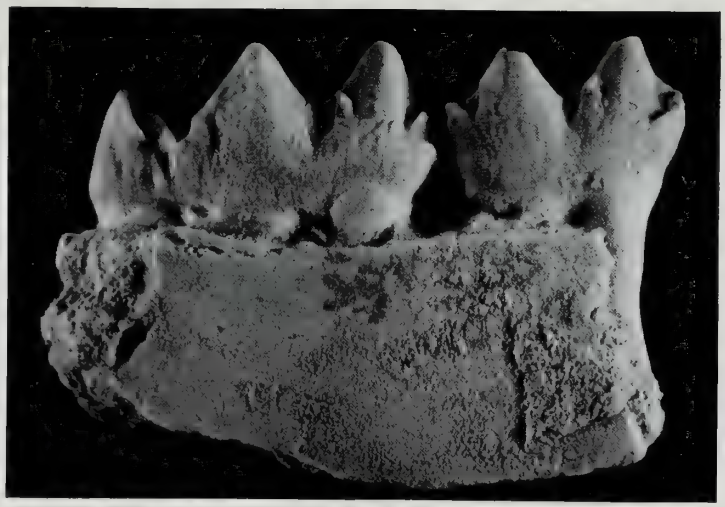

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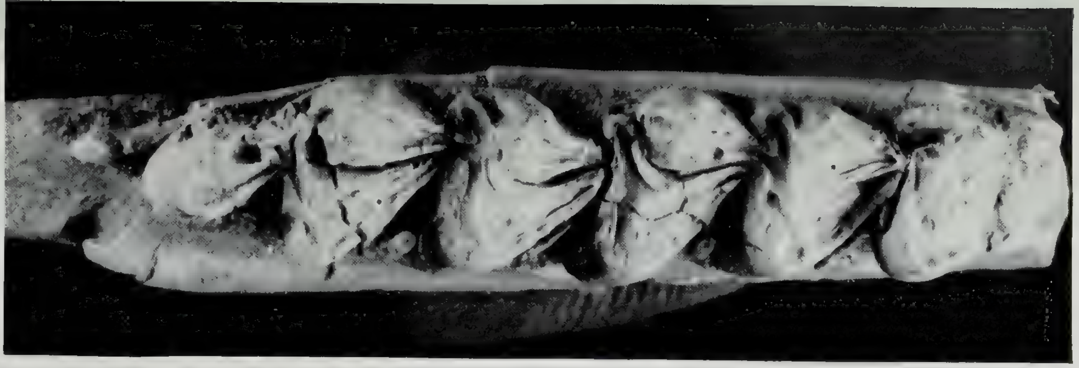
PLATE 14

Fig. 1. ***Propalaeoryx nyanzae*** Whitworth 1958. Right M_2 and M_3; occlusal aspect. (K.774.52) ×2·9 approx.

Fig. 2. ***Propalaeoryx nyzanzae*** Whitworth 1958. Left M^1 and P^4; occlusal aspect. (K.Mt.67.51) ×2·9 approx.

Fig. 3. ***Propalaeoryx nyzanzae*** Whitworth 1958. Left M^1 and P^4; lingual aspect. (K.Mt.67.51) ×2·9 approx.



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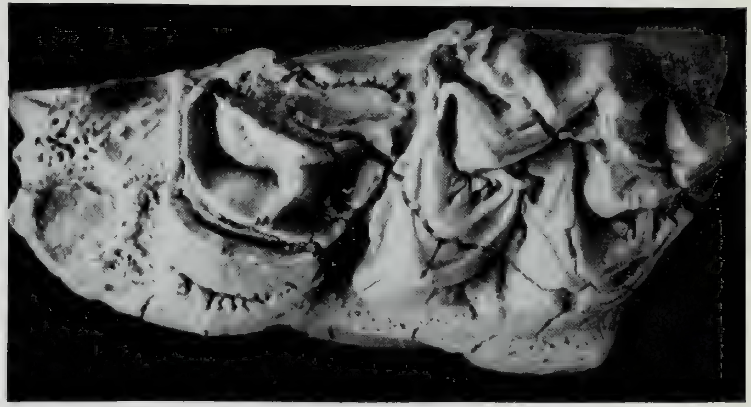

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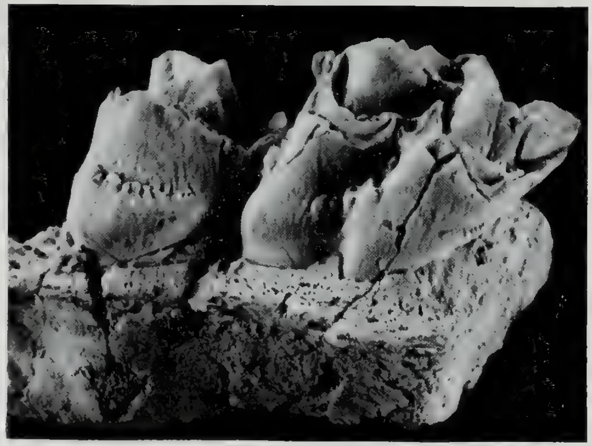

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THE AFFINITIES OF *HALCYORNIS* FROM THE LOWER EOCENE

C. J. O. HARRISON

AND

C. A. WALKER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 21 No. 4
LONDON : 1972

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THE AFFINITIES OF *HALCYORNIS* FROM THE LOWER EOCENE

BY
COLIN JAMES OLIVER HARRISON
AND
CYRIL ALEXANDER WALKER

Pp. 151–169; 3 *Plates*, 9 *Text-figures*

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By C. J. O. HARRISON & C. A. WALKER

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SYNOPSIS

Halcyornis toliapicus (Koenig) of the Lower Eocene, known from a single cranium, has been classified with the gulls (Koenig, 1825 and Lydekker, 1891) and the kingfishers (Owen, 1846). The specimen has now been fully prepared; it is redescribed here and its probable affinities re-appraised on the characters now apparent.

A comparison with Recent forms indicates a general similarity to skulls of Coraciiformes and Piciformes. A more detailed examination of a range of species representing families within those two orders indicates that the greatest similarity is to the Coraciiformes, particularly to the rollers of the Coraciidae and Leptosomatidae. The characters of the fossil specimen do not appear to indicate stronger affinities with either one of those families, however, and it is therefore proposed that *Halcyornis* should be regarded as the type- (and only known) genus of a new family within the Coraciiformes. A diagnosis is given of the Halcyornithidae.

I. HISTORICAL INTRODUCTION

In the earlier part of the 19th century the cranial portion of a small bird skull was found in the London Clay, Ypresian (Lower Eocene) of the Isle of Sheppey, Kent, England. It was figured by Koenig (1825), who noted the general resemblance of the rounded cranium with its even, tapering temporal fossae to that of some of the smaller gulls (e.g. *Larus canus* or *L. ridibundus*) and therefore reconstructed it as a small gull, calling it *Larus toliapicus*.

Owen examined the specimen, and noted (1846 : 554) the absence of the supra-orbital grooves which accommodate the lacrimal glands (grooves which are normally present in, and typical of, gulls and most other sea-birds). He compared the specimen with Recent material but may have used an incomplete collection. He noted the resemblance of the temporal fossae to those of the kingfisher, *Alcedo atthis* (although in the latter the fossae extend upwards until they almost meet in the mid-line) and, believing that it was probably an early kingfisher, called it, '*Halcyornis toliapicus*. Bird probably of the family Halcyonidae'. The kingfisher family is now known as the Alcedinidae.

Lydekker (1891 : 183) considered the specimen to be a gull. He rejected Owen's suggestion because the temporal fossae on the posterior part of the cranium were further apart than in the kingfisher; and also because of the narrowness of the interorbital bar formed by the frontal bones. He commented that, 'the imperfection of the fronto-parietal region renders it difficult to be sure as to the presence of superorbital grooves, but the appearance suggests their presence'. He associated with the skull the distal end of a left humerus (BMNH No. A 10) which he considered to be of larid origin. There appears to be no reason for associating the humerus with the cranium; the former has therefore been considered as a separate specimen and has not been dealt with in the present paper.

We have compared *Halcyornis* with a range of Recent bird bones in the British Museum (Natural History). The most obvious character, and the one on which earlier identifications were based, is the presence of well-defined temporal fossae which occupy about two-thirds of the total width of the cranium. They are of fairly even shape, tapering posteriorly, with a slightly concave posterior margin. The search for similar Recent species showing this type of posteriorly-rounded cranium with relatively simple temporal fossae produced a number of alternative possibilities, allowance having been made for a reasonable degree of variation. Specimens with some similarity were found in the Procellariidae (Procellariiformes), Fregatidae (Pelecaniformes), Rhinochetidae (Gruiformes), Laridae (Charadriiformes), Cuculidae (Cuculiformes), Alcedinidae, Momotidae, Meropidae, Coraciidae, Upupidae, Leptosomatidae (Coraciiformes), Galbulidae, Bucconidae, Capitonidae, and Ramphastidae (Piciformes). So many families possess this type of skull that it is obviously an unsatisfactory character from the taxonomic point of view, but nevertheless provides an initial limited list of potentially related families

II. DESCRIPTION AND STATE OF PRESERVATION

It was necessary to consider the other characters of the specimen, which was further prepared for this purpose, making some of the interorbital features more apparent.

The specimen consists of the posterior portion of a cranium, imperfect in all its aspects. The roof has been broken away to show part of the endocranial cast and the anterior region is broken off about half-way along the frontals. The interorbital bar is narrow; the orbital rim is apparently undamaged, with no evidence of any superorbital grooves. There is a fairly large, well-marked temporal fossa the margin of which arises anteriorly at the junction between the postorbital processes and the orbital rim, runs obliquely backwards towards the mid-line, and then curves round to pass outwards along the dorsal border of the occiput.

In lateral view the skull shows a cranium that is not particularly inflated or rounded, and the thick interorbital septum is perforated only by a single foramen for the optic nerve. This foramen is situated at the postero-ventral corner and is rather small. The orbital rim is raised slightly above the plane of the skull roof. The postorbital processes are broken on both sides, but would have been blade-like, with narrow edges directed laterally. The temporal fossa forms, in this aspect, a well-marked groove between the postorbital process and the tympanic cavity.

The palatal surface is eroded and much of the detail on the basiparasphenoid region has been lost. The rostroparasphenoid is thick and the alaparasphenoids swing out to form a wide angle with the former. The eustachian tubes are visible. There is a well-marked depression just posterior to the ridge which runs across and joins the two alaparasphenoids. Much of the basioccipital is broken, but the occipital condyle, although eroded, is still present and was small. The foramen magnum is directed posteroventrally, but its exact shape is impossible to determine. The profile of the occiput in this view is relatively flat with a slight swelling around the foramen magnum.

The occiput is also damaged about the mid-line, but the shape is broadly crescentic, with a well-defined median ridge running down the parietals and supraoccipital to meet the dorsal rim of the foramen magnum in the mid-line. Either side of this ridge there is a well-marked groove, which probably indicates the border between the supraoccipital and opisthotic. There appear to have been no foramina in the supraoccipital. The temporal fossae are distinct from this angle and their posterior border forms a well-defined ridge along the upper edge of the occiput. The fossae do not, however approach the mid-line.

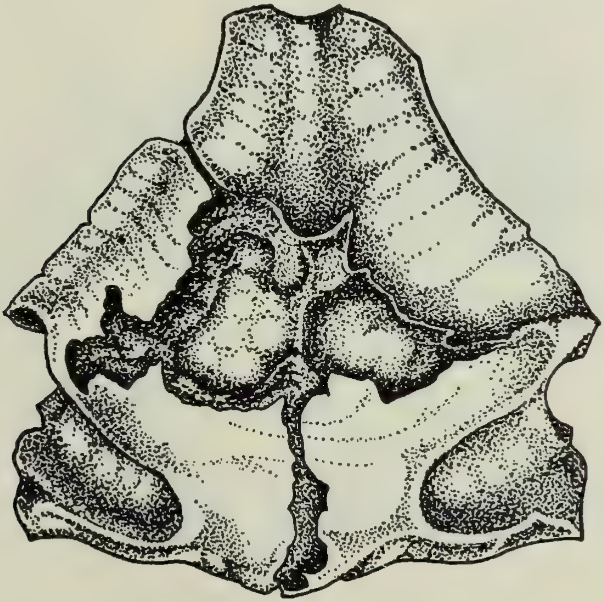

FIG. 1. *Halcyornis toliapicus*. BM(NH) No. A 130. Cranium. Dorsal View, ×4.

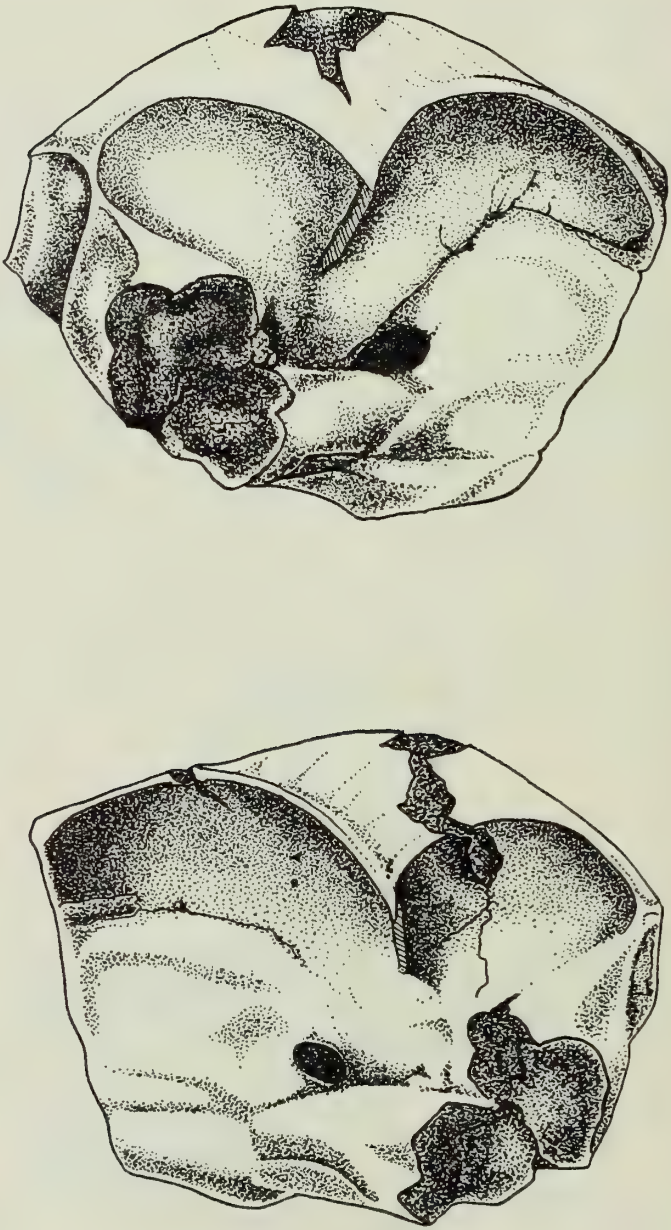

FIG. 2. *Halcyornis toliapicus*. BM(NH) No. A 130. Cranium. Lateral View, × 4.

MEASUREMENTS

Maximum width across exoccipital region	20·5 mm
Minimum width between temporal fossae	9 mm
Width between postorbitals	22 mm
Width of interorbital bar	7 mm
Minimum width of interorbital septum	2 mm
Maximum depth of skull in orbital region	17 mm
Maximum length of auditory meatus	9 mm

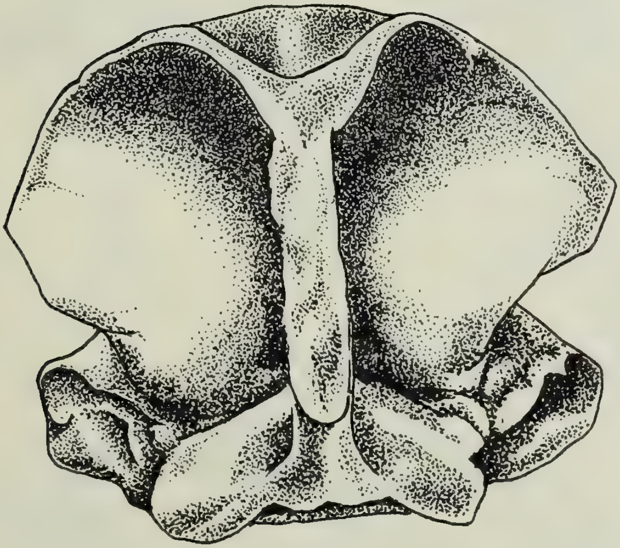

FIG. 3. *Halcyornis toliapicus*. BM(NH) No. A 130. Cranium. Frontal View, × 4.

III. COMPARISON WITH RECENT FORMS

From the description it is apparent that for determining relationships, characters might be used other than those used in the past. The most obvious of these relate to:

1. The upper edges of the orbit.
2. The interorbital septum and foramen.
3. The relative size and shape of the parasphenoid region.

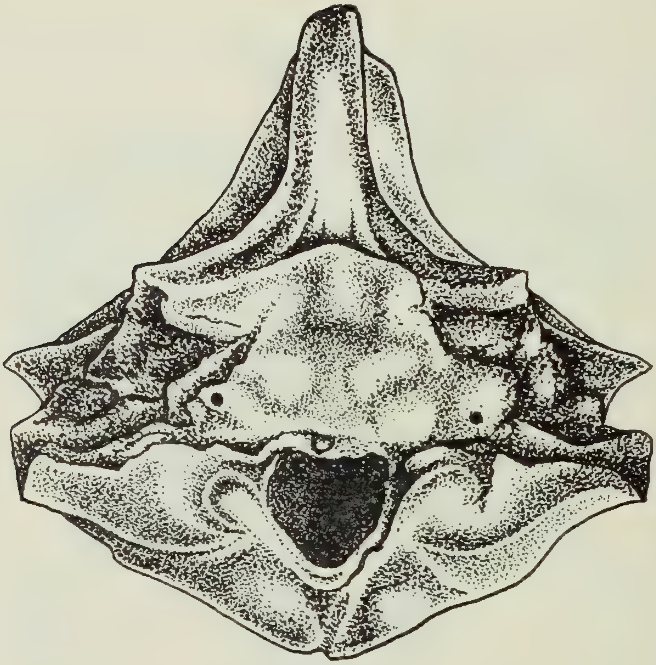

FIG. 4. *Halcyornis toliapicus.* BM(NH) No. A 130. Cranium. Ventral View, × 4.

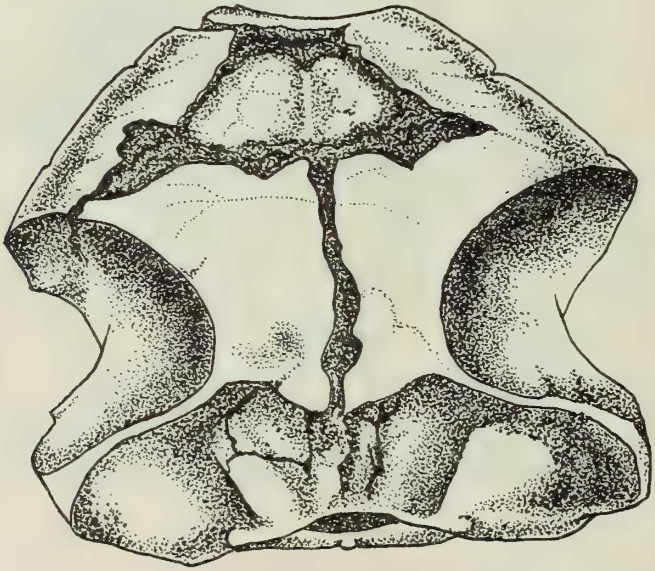

FIG. 5. *Halcyornis toliapicus.* BM(NH) No. A 130. Cranium. Posterior View, × 4

1. *The edges of the orbit*

Lydekker's views on the affinities of *Halcyornis* appear to have been strongly influenced by his opinion that the appearance suggested the presence of supraorbital grooves, subsequently destroyed. On birds which normally live on or by salt water,

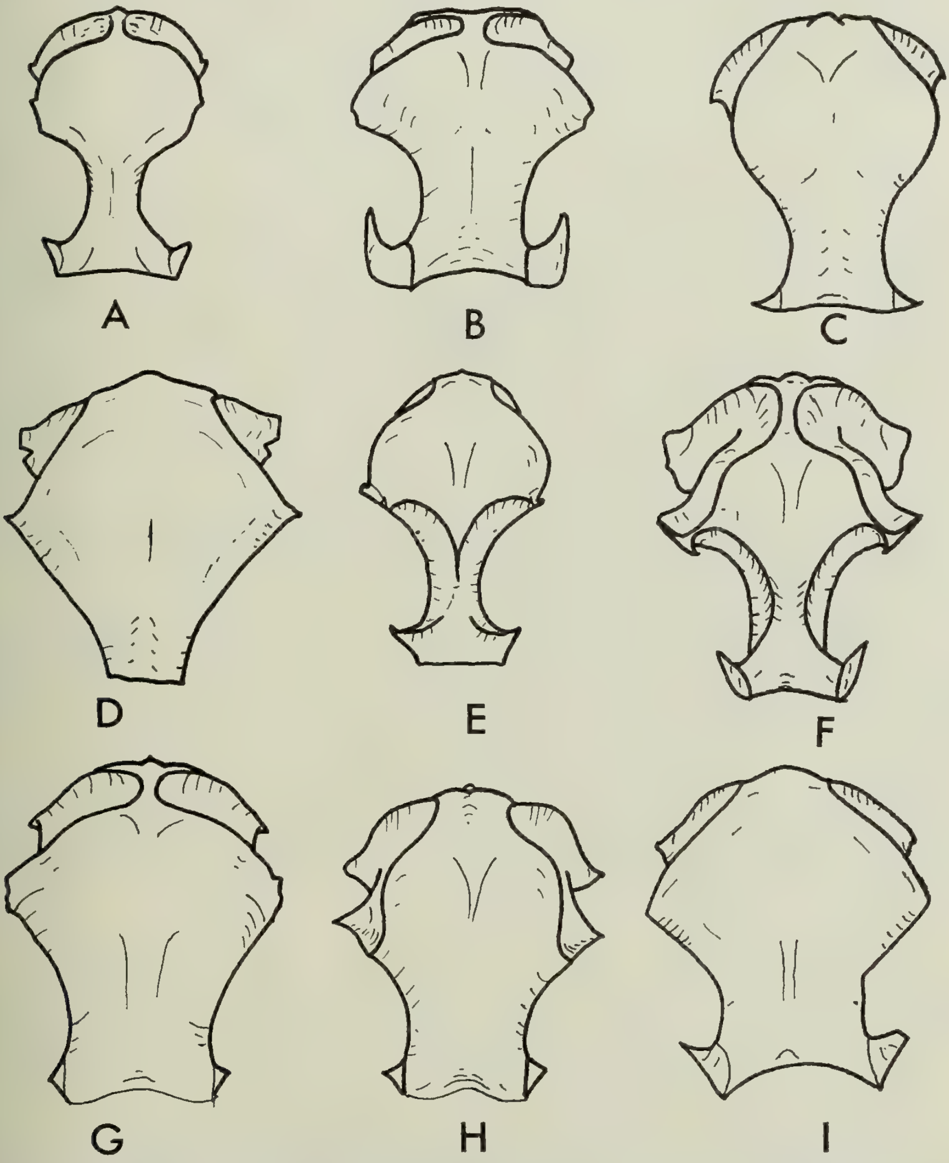

Fig. 6. Diagrams of dorsal views of crania to show width of interorbital bridge. A, *Alcedo*; B, *Dacelo*; C, *Coccyzus*; D, *Halcyornis*; E, *Larus*: F, *Puffinus*; G, *Rhynochetos*; H, *Fregata*; I, *Coracias*.

the supraorbital glands tend to become greatly enlarged and are housed in distinct grooves along the upper edges of the orbits (Text-fig. 6E, F). These glands, which assist salt-excretion, are much smaller in related fresh-water species. The grooves, where present, are on top of the skull and tend to occupy most of the upper edges of the orbits, reducing the thickness of the frontal bones in this region. They may be deepest towards the centre of their width, at times penetrating to the orbits below and forming a series of fenestrae, or they may give to the orbital edges an irregular or eroded appearance. A consistent feature is the distinct ridge of bone along the inner edge of each groove where the frontal bone is restored to its normal thickness.

Since these ridges of bone are not apparent on *Halcyornis* it would be necessary, were it held that supraorbital grooves had been present, to assume that the entire bony shelf supporting the supraorbital glands had worn away completely, back to this ridge. Although the presence of the groove reduces the thickness of the frontal bone by removing part of its upper surface, it does not affect the underlying surface within the orbit which curves downwards away from the orbit edge in the normal manner; and therefore an orbit worn back to the inner edge of a supraorbital groove would show a considerable depth of worn or broken surface at the edge between the top of the skull and the inside of the orbit. The skull of *Halcyornis* does not; the upper edge of the orbit does not taper to a very narrow edge but shows an abrupt surface about one millimetre deep, suggesting that a small amount of wear may have occurred on a normal orbit lacking a supraorbital groove (Text-fig. 2A, B). Another character of the supraorbital grooves is that it tends to terminate rather abruptly posteriorly, with the inner ridge curving towards the orbit edge; thus if a groove were to wear away, the orbit edge would show a sharp discontinuity at this point. There is no such discontinuity in *Halcyornis*.

The absence of a supraorbital groove suggests that the specimen is not related to the Procellariiformes, Anseriformes or Charadriiformes (including Laridae). The Pelecaniformes (Text-fig. 6H) and Ciconiiformes, although in some cases associated with salt water, do not possess these supraorbital grooves. Since the groove is a relatively plastic and adaptable character in the families in which it now occurs, it might be argued that it could have been absent in some or all species in earlier epochs. It is known to be present in Miocene gulls but we have no definite proof that it was present earlier, and as an indication of relationship it can be assessed only in conjunction with other characters.

2. *The interorbital septum*

Halcyornis has a thick, unfenestrated interorbital septum (Text-fig. 3) with a single optic foramen in a low posterior position (Text-fig. 7I). Most of the birds discussed in this paper have marked and often extensive interorbital fenestrae (Text-fig. 7); these include the Procellariiformes, Pelecaniformes, Ciconiiformes and Charadriiformes. In the skimmers (*Rhynchops* spp., Charadriiformes) a highly specialized method of feeding (Zusi, 1962) has necessitated extra strengthening of the skull, including the development of a thick, solid interorbital septum; the latter, however, is pierced by the optic foramen in a high position (Text-fig. 7C) and there are small paired fenestrae opening into the cranial cavity just above this. Interorbital fenestrae are also present in the Rhinochetidae, Cuculidae, and Alcedinidae. On the other hand the coraciiform and piciform families listed earlier generally show a solid interorbital septum with a low posterior optic foramen like that of *Halcyornis*; the only exceptions are the Upupidae with a pair of fenestrae opening into the cranial cavity from the upper orbits and the Momotidae with a tiny variable "relict" foramen in the mid-septum. On the basis of this character there is a strong case for linking *Halcyornis* with the Coraciiformes and Piciformes, although the example of *Rhynchops* indicates that exceptional circumstances could lead to some adaptive variation in the fenestration of the septum.

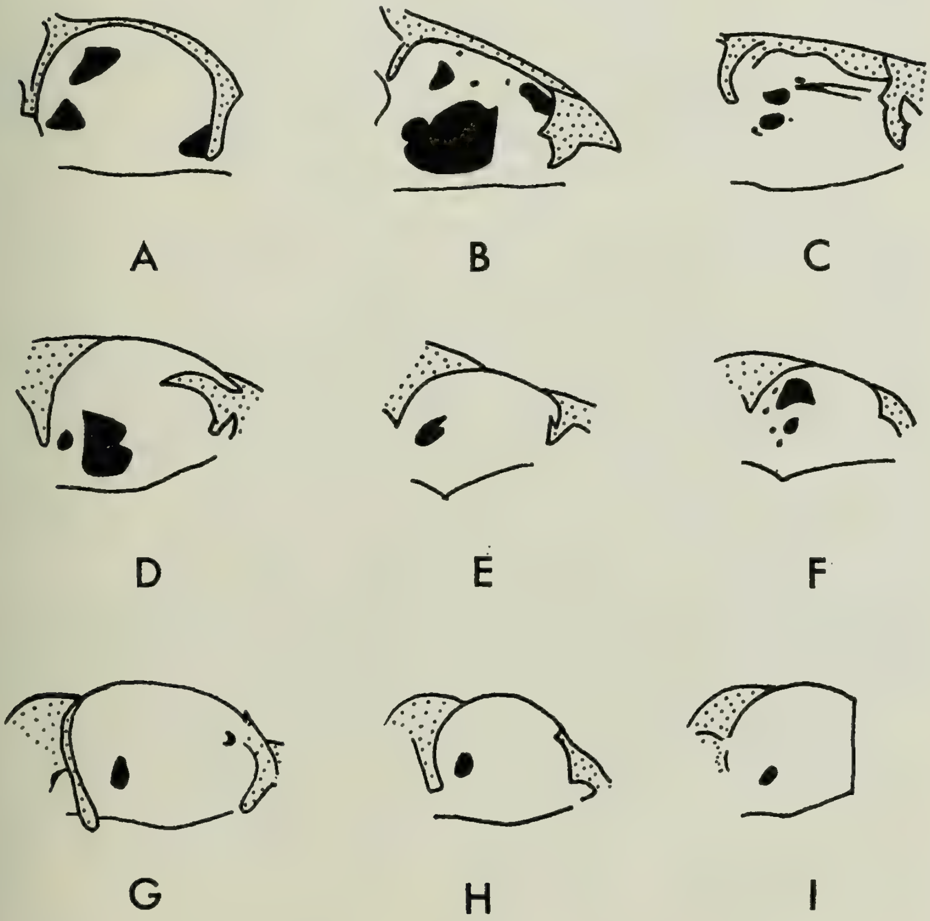

Fig. 7. Diagrams to show interorbital septa and position and size of interorbital foramina. A, *Fregata*; B, *Puffinus*; C, *Rhynchops*; D, *Dacelo*; E, *Merops*; F, *Upupa*; G, *Leptosomus*; H, *Eurystomus*; I, *Halcyornis*.

Another character in which *Halcyornis* resembles species of the Coraciiformes and Piciformes is the shape of the angle formed by the interorbital septum and the underside of the interorbital bridge section of the frontals (Text-fig. 8). On most of the Recent species examined the interorbital bridge is relatively thin and the septum extends well up towards the orbit where it meets the underside of the frontal at a sharp angle. In *Halcyornis* the interorbital bridge is much thicker towards the mid-line and tapers down more gradually, making an obvious junction with the septum at about a third of the distance between the top of the bridge and the base of the septum (Text-figs 2A, 2B, 3). This is less obvious anteriorly where the bone narrows, but can be clearly seen in lateral view as a discontinuity crossing the inner orbit. This heavier tapering interorbital bridge is apparent on skulls of *Momotus* (Coraciiformes) and *Megalaima*, *Selenidera* and *Monasa* (Piciformes). *Eurystomus*, *Leptosomus* and *Merops* (all Coraciiformes) show a similar low junction between septum and frontal inside the orbit; in these genera, however, there is a mid-line hollow on the top of the skull and the frontal is concave in cross-section, so that the apparently lower position of the junction is due to a general ventral displacement and cannot be regarded as an homologous development.

3. *The parasphenoid region*

We have followed Jollie (1957) in regarding the externally visible ventral bones of the hind-skull as parasphenoid rather than sphenoid. The basiparasphenoid of *Halcyornis* is transversely elongated and roughly oblong, with a slight lateral taper (Text-fig. 4, Pls 1B, 3E). It is rather flat and this may have been emphasized by pressure and slight erosion. Anteriorly it terminates in a distinct edge where it abuts on the alaparasphenoids. The rostroparasphenoid is thick and has a small but distinct ventral prominence near the posterior end. The most conspicuous feature on each side is the alaparasphenoid, directed strongly laterally at the hind end of the rostroparasphenoid to form a prominent bulging ridge at the back of the base of the orbit, curving upwards to meet the orbitosphenoid. The lateral ends of both alaparasphenoids and the basiparasphenoids are broken away.

In the Procellariformes (Pl. 3C) the basiparasphenoid tapers markedly towards the front and there is a narrow gap between it and the ventrally projecting edge of what appears to be the orbitosphenoid. The Pelicaniformes show a tapering basiparasphenoid which becomes distinctly wedge-shaped in some forms, and in *Fregata* (Pl. 3B) there is again a gap between the basiparasphenoid and orbitosphenoid. In the Charadriiformes (Pl. 3D, F) this anterior taper is again apparent on the basiparasphenoid, while the alaparasphenoid is more prominent than in the previous taxa but slants away weakly to the orbital and otic region, least so in some small *Larus* species such as *L. ridibundus*. The Cuculiformes (Pl. 3L) show a wedge-shaped basiparasphenoid, narrow anteriorly in some species but broad in others, and the alaparasphenoid is poorly defined.

In these characters, as in the previous ones, the greatest similarity to *Halcyornis* is shown by piciform and coraciiform birds. In most of these the basiparasphenoid is wide transversely, tending towards an oblong shape with little lateral taper; in the Capitonidae (Piciformes) and in the Coraciidae (Pl. 3H) Leptosomatidae, and

Momotidae (Coraciiformes) it has a similar shape to the fossil, but in the Bucconidae (Pl. 3I) and Galbulidae (Piciformes) and in the Alcedinidae (Pl. 3J) and Meropidae (Pl. 3G) (Coraciiformes) the distance between the orbits and the foramen magnum is shortened, making the basiparasphenoid narrower from front to back.

In both orders many species have a pair of small prominences on the ventral surface of the basiparasphenoids. These are very variable, being almost absent, for instance, on *Alcedo* (Alcedinidae). In *Halcyornis* this bone shows a pair of small areas with dull surfaces suggesting abrasion or heavy pressure, corresponding in position to these prominences although one is a little displaced by fracture.

The principal difference between the Piciformes and Coraciiformes lies in the development of the Alaparasphenoid. On the piciform skulls examined this element is barely apparent, although there is a small, poorly developed ridge on the skulls of the larger *Megalaima* species. In the Coraciiformes the alaparasphenoid shows some variation in development in the Meropidae, Leptosomatidae, and many of the Coraciidae it is well developed, as a distinct projecting ridge at the posterior basal edge of the orbit, the resemblance to *Halcyornis* being especially strong in the rollers *Leptosomus*, *Eurystomus* and *Coracias*.

In both orders the rostroparasphenoid is relatively stout; *Merops* (Meropidae) and *Dacelo* (Alcedinidae) show a ventral prominence near the posterior end which is like that on the fossil.

Conclusions

The characters of *Halcyornis* listed above afford no good reason for linking it with either the Laridae or the Charadriiformes. The only orders with which it appears to show any consistent affinities are the Piciformes and the Coraciiformes; insofar as the parasphenoid region is concerned it seems more like the Coraciiformes, in particular the Coraciidae and the Meropidae.

IV. DETAILED COMPARISON WITH CORACIIFORM AND PICIFORM SPECIES

The species within these two orders do not show uniform skull characters, for they have evolved differences in feeding habits and bill-shape and therefore exhibit varying degrees of divergence from a hypothetical ancestral form. Specimens of the following species were used in this comparison:

CORACIIFORMES
- Alcedinidae
    - *Dacelo novaeguineae*
    - *Alcedo atthis*
- Momotidae
    - *Momotus* sp.
    - *Aspatha gularis*
    - *Baryphthengus ruficapillus*
- Meropidae
    - *Merops apiaster*

- Leptosomatidae
  - *Leptosomus discolor*
- Coraciidae
  - *Atelornis pittoides*
  - *Coracias garrulus*
  - *Eurystomus glaucurus*
- Upupidae
  - *Upupa epops*

PICIFORMES

- Galbulidae
  - *Galbula leucogastra*
- Bucconidae
  - *Monasa morphoeus*
- Capitonidae
  - *Megalaima virens*
  - *M. haematocephala*
- Ramphastidae
  - *Selenidera langsdorffi*

1. *Cranial shape*

The general roundness of the fossil cranium in lateral view (Text-fig. 2A, B) is similar to that of *Monasa morphoeus*, *Megalaima haematocephala* (Text-fig. 8B), *Selenidera langsdorffi* and the Momotidae species. Most of the others have a cranium extending further back and with a slight upward taper, apparently caused by a forward shift of the foramen magnum and a shortening of the basiparasphenoid area so that the occiput faces more ventrally. This shift of the foramen would seem to be linked with a more upright perching stance by the bird. In *Leptosomus* and *Eurystomus* this shift is accompanied by a shortening of the cranium but this appears to be compensated for by an increase in the height, the cranium bulging noticeably at the top. In *Upupa* there is no apparent shift but the cranium is generally enlarged and rounded.

2. *Temporal fossae*

It has already been indicated that the size and shape of the temporal fossae (site of origin of the M. adductor mandibulae externus) varies considerably from species to species. The two examples of *Megalaima* demonstrate this. The fossae of the smaller species (*M. haematocephala*, Text-fig. 8B) are little larger than those of *Halcyornis*, but those of the larger bird (*M. virens*, Text-fig. 8D) are considerably elongated and extend across to meet at the back of the skull. In the Coraciiformes small fossae similar in size to those of *Halcyornis* but differing a little in shape occur on the various Momotidae species (Text-fig. 8C). In *Leptosomus* they are also small, but on other species show a variable tendency to become elongated towards the mid-line, almost meeting in *Atelornis pittoides* and the Alcedinidae (Text-figs 6B, 8F). The temporal fossae of *Halcyornis* extend well forwards anterodorsally, approaching the orbit closely and reducing the spur above the postorbital process to a narrow ridge. A slight discontinuity in the floor of the fossae, adjacent to the process, seems to indicate a secondary area of muscle attachment, probably of the M. dermotemporalis, an accessory muscle of the neck used in head movements. This area is relatively poorly developed in most of the forms considered here but is rather more apparent in *Megalaima haematocephala, Monasa morphoeus* and *Upupa epops,* although very shallow in *Upupa*. The narrower ridge of the postorbital process in *Leptosomus discolor* and *Selenidera langsdorffi* appears to be due to an

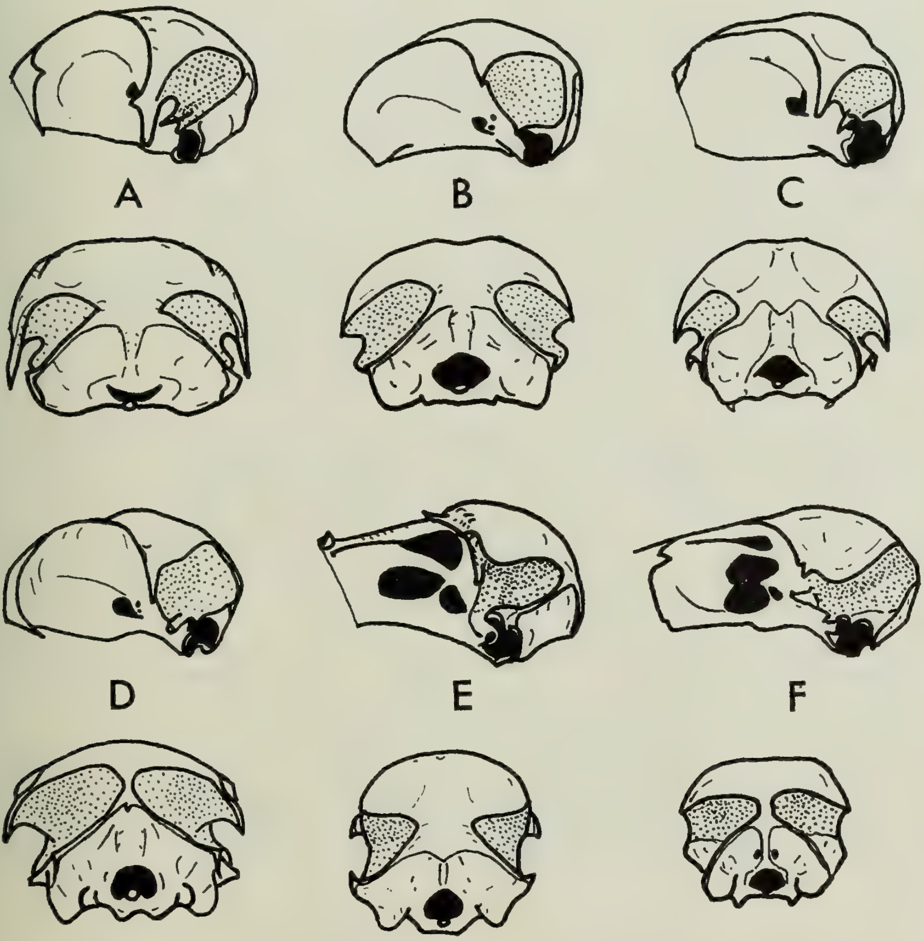

FIG. 8. Diagrams of left lateral posterior views of crania to show variation and extent of temporal fossae. A, *Coracias*; B, *Megalaima haematocephala*; C, *Momotus*; D, *Megalaima virens*; E, *Larus*; F, *Alcedo*.

increase in the M. adductor mandibulae externus rather than M. dermotemporalis. The relatively small size of the M. dermotemporalis in the species which actively hunt live prey, and its development in species which tend to take insects from a solid substrate or to take fruit, suggests that the relatively plastic shape of the fossae is linked with the type of feeding behaviour.

3. *Interorbital bridge and dorsal groove*

Dorsally the cranium of *Halcyornis* tapers to a relatively narrow interorbital bridge formed by the frontals (Text-fig. 1), and there is a distinct groove along the mid-line (Text-fig. 3, Pl. 1A). The skull roof also bears a series of fine striae radiating from the edges of the orbits, mostly directed posteriorly (Text-fig. 1).

Over the two orders as a whole the trend appears to be for the interorbital bridge to become gradually broader (Text-fig. 6). The bridge is fairly narrow on *Aspatha gularis* and *Atelornis pittoides*, but only in *Blcedo atthis* (Text-fig. 6A) does it approach the narrowness of *Halcyornis*. Milne-Edwards and Grandidier's (1876) plate of the skull of the Madagascan Roller, *Bractypteracias leptosomus* (Coraciidae), shows that this too had a narrow interorbital bridge. In the Alcedinidae the width of the bridge varies (Text-fig. 6A, B), the narrow bridge apparently correlated with a slender bill. The dorsal groove is apparent in species of Momotidae, Alcedinidae, Upupidae, Leptosomidae and most Coraciidae; poorly defined in *Atelornis pittoides*, *Monasa morphoeus* and *Merops apiaster*; virtually absent in the Ramphastidae;

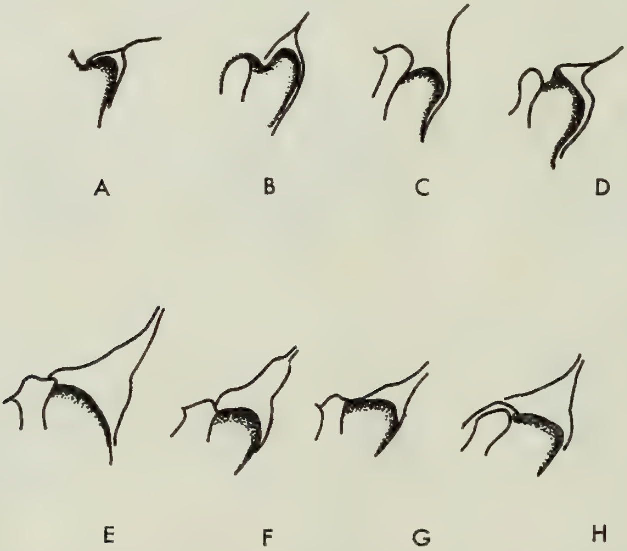

FIG. 9. Diagrams of the left external auditory meatus. A, *Halcyornis*; B, *Eurystomus glaucurus*; C, *Leptosomus discolor*; D, *Coracias garrulus*; E, *Dacelo novaeguineae*; F, *Megalaima virens*; G, *Monasa morphoeus*; H, *Momotus martii*; approx. ½ nat. size.

and replaced by a ridge in the Galbulidae and Capitonidae. The striae, which we suspect may vary with age and the degree of ossification, are more or less apparent in most of these species.

4. *Occipital region*

The fossil shows a very definite curved occiput of fairly even width (Pl. 1C). The lateral ends (formed by the exoccipitals) terminate in a narrow ridge which is also the posterior edge of the auditory meatus, and this ridge curves abruptly at the top to form a small arch almost at the point where the ridge of the upper edge of the occiput terminates.

Most of the skulls examined show an occiput similar to that of *Halcyornis*, but its degree of curvature varies from one species to another. On most of them the ridge of the upper edge of the occiput terminates laterally in a triangular-shaped surface which slopes down towards the meatus, the upper arch of which is less acute than in *Halcyornis*, lower and more anterior in relation to the exoccipitals. The rollers *Eurystomus glaucurus* and *Coracias garrulus* (Text-fig. 8A), however, are much more like *Halcyornis*. Firstly, the occiput is very similar in shape and relative size; secondly, in *E. glaucurus* and to some extent in *C. garrulus* the triangular surface is very small and the upper edge of the meatus terminates in a small acute arch, near the end of the occipital ridge, very similar to that of *Halcyornis* (Text-fig. 9). In the latter some allowance must be made for probable erosion of these surfaces.

V. POSSIBLE CHARACTERS OF *HALCYORNIS*

When a fossil bird is known only from an incomplete skull, any ideas concerning its appearance or habits must necessarily be highly conjectural. It is, however, possible to make a few intelligent guesses by extrapolation from Recent species. The size of the fossil skull, compared with those of other birds, suggests that *Halcyornis* was probably about the size of a medium-sized thrush (*Turdus* sp.). The position of the foramen magnum suggests that the bird did not have the very upright posture of the present-day rollers (Coraciidae) and kingfishers (Alecinindae) but probably adopted a more horizontal body posture on a perch or on the ground, like that of the smaller barbets (Capitonidae). The narrow bridge between the orbits suggests that the bill was probably slender and more like a typical kingfisher's than a roller's. Most birds of this type which catch living food by rapid and vigorous movements have temporal fossae extending well back around the skull; but the temporal fossae of *Halcyornis* are fairly small and rounded, suggesting that this species may have taken food, probably small creatures or fruit, from the substrate or from the surfaces of vegetation rather than by seizing it rapidly in the air.

VI. GENERAL CONCLUSIONS

From an examination of affinities within the higher taxa it is apparent that *Halcyornis toliapicus* has been wrongly assigned to the Laridae and that its true affinities seem to lie with the Coraciiformes and Piciformes, more specifically with the former. The subsequent comparison with families within those two orders appears to confirm that conclusion and to reinforce the view that the closest affinities are with the Coraciidae. The similarities are not sufficient, however, to justify referring it to that family, and it appears to show the characters of several families, and also exhibits its own peculiarities and combination of characters. Hitherto Coraciiformes have not been described from the Lower Eocene, but the momotid *Uintornis*[1] has been described from the middle Eocene of Wyoming, the bucerotid *Geisleroceros* from the Middle Eocene of Germany, the coraciid *Geranopterus* from the Upper Eocene of France, and the alcedinid *Protornis* from the Upper Eocene of Switzerland. *Halcyornis*, because of its earlier origin, might be a representative of a group ancestral to more than one of the Recent families. As a matter of taxonomic convenience it seems best for the present to treat *Halcyornis* as the unique representative of a new family of the Coraciiformes, systematically not far removed from the Coraciidae: the Halcyornithidae.

VII. SYSTEMATIC DESCRIPTION

Order CORACIIFORMES

Family **HALCYORNITHIDAE** nov.

Family diagnosis: Cranium not particularly inflated or rounded. Interorbital bar narrow and deep. Postorbital process small and narrow. Temporal fossae tapering posteriorly, occupying about two-thirds of total width of cranium, slightly curved where they border the edge of exoccipital region. Occiput semi-lunar with well-defined median ridge on parietals. Interorbital septum thick, with single optic foramen in low position. Wide angle between alaparasphenoids and rostroparasphenoid, latter thick.

Genus ***HALCYORNIS*** Owen, 1846

Diagnosis: The only genus of its family.

Type species: *Halcyornis toliapicus* (Koenig).

Halcyornis toliapicus (Koenig, 1825)
(Pls 1–3; Text-figs 1–9)

1825 *Larus toliapicus* Koenig, pl. 16, fig. 193.
1846 *Halcyornis toliapicus* (Koenig): Owen: 554.

Diagnosis: The only species of the genus.

Holotype: Imperfect cranium in Brit. Mus. (Nat. Hist.) No. A 130.

Locality and horizon: London Clay (Ypresian), Lower Eocene of Sheppey, Kent, England.

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[1] According to Dr. J. Cracraft (*pers. comm.*), *Uintornis* is not a motmot.

VIII. ACKNOWLEDGEMENTS

We wish to thank Dr. A. J. Charig and Dr. J. Cracraft for criticizing the manuscript; Mrs. T. E. D. Brendell for making the detailed line drawings; Mr. F. Howie for preparing the specimen and Mr. T. W. Parmenter for taking the photographs.

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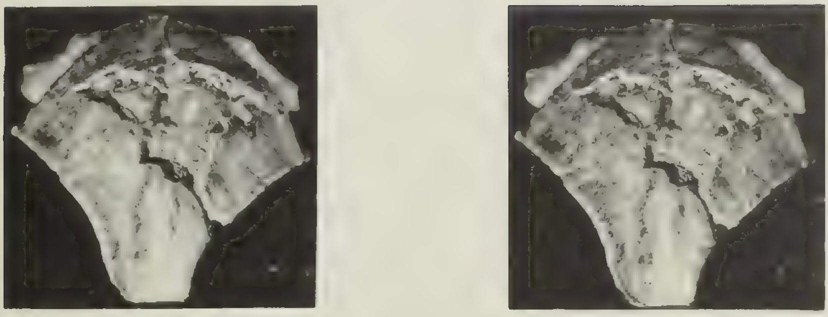
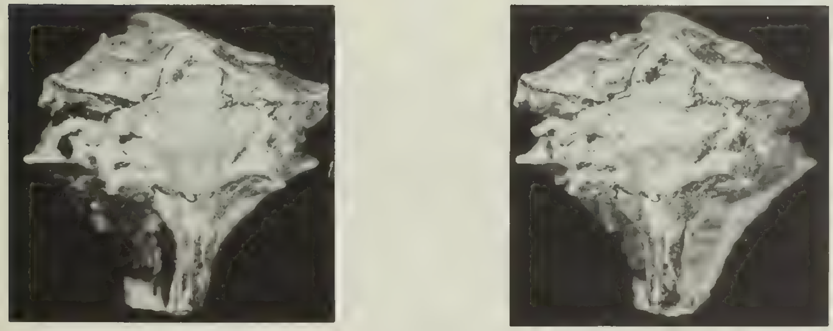
PLATE 1

Halcyornis toliapicus BM(NH) No. A 130.
Stereo views of cranium, × 2.
A, dorsal; B, ventral; C, posterior.



A



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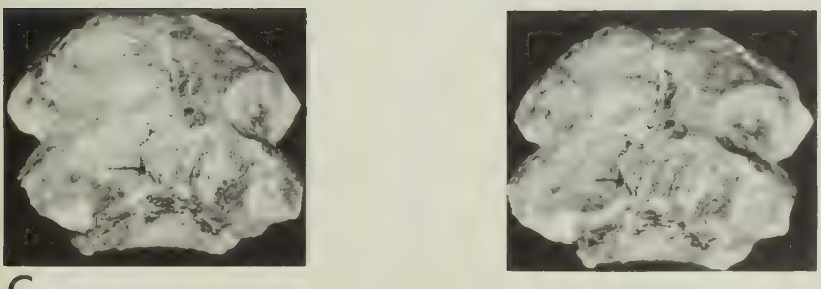

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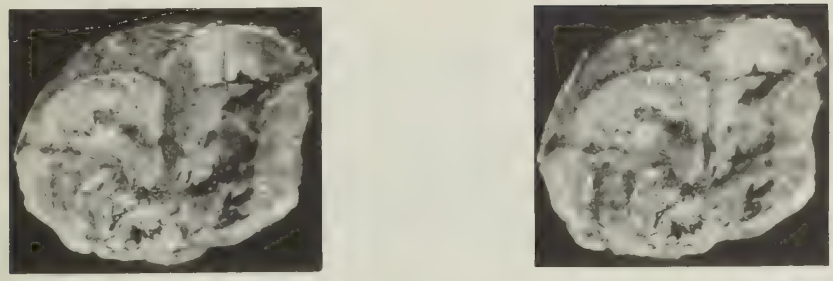
PLATE 2

Halcyornis toliapicus BM(NH) No. A 130.
Stereo views of cranium, × 2.
A, right lateral; B, left lateral; C, frontal.



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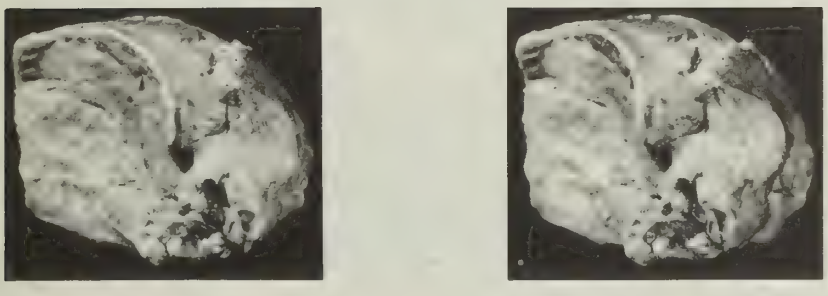

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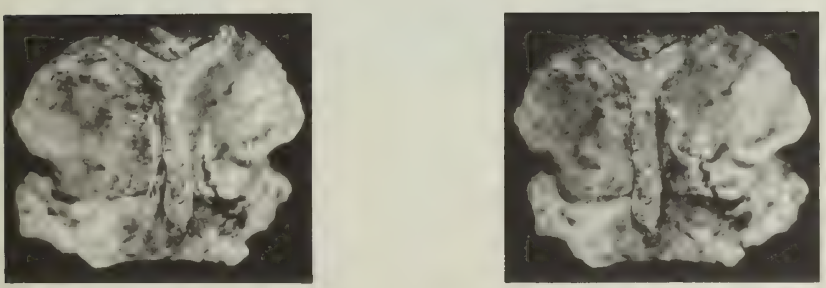

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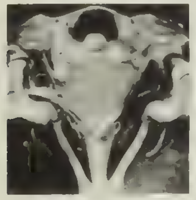
PLATE 3

Ventral views of bird crania to show variations in basisphenoid elements.

A, ***Rhynochetos jubatus***
B, ***Fregata ariel***
C, ***Puffinus diomedia***
D, ***Larus argentatus***
E, ***Halcyornis***
F, ***Rhynchops niger***
G, ***Merops apiaster***
H, ***Coracias garrulus***
I, ***Monasa morphoeus***
J, ***Dacelo novaeguineae***
K, ***Upupa epops***
L, ***Coccyzus erythropthalmus***
various magnifications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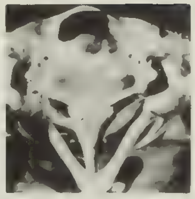
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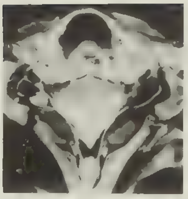
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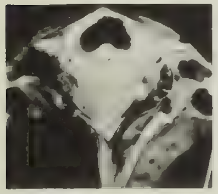
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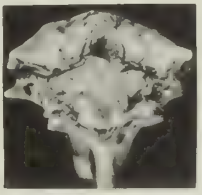
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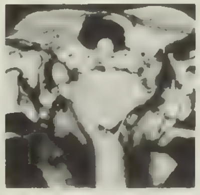
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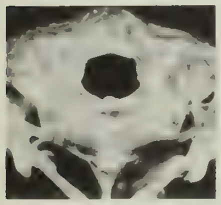
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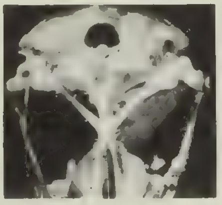
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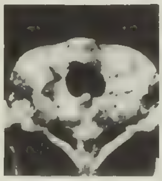
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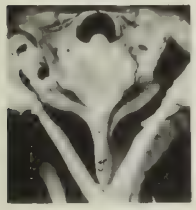
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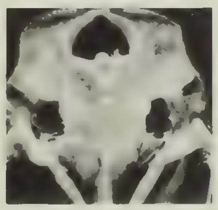
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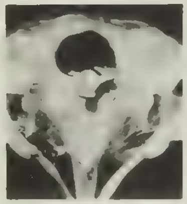
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DINOFLAGELLATE CYSTS AND ACRITARCHS FROM THE KIMMERIDGIAN (UPPER JURASSIC) OF ENGLAND, SCOTLAND AND FRANCE

G. U. GITMEZ
AND
W. A. S. SARJEANT

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NATURAL HISTORY

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Pp. 171–257; 17 *Plates*; 27 *Text-figures*; 6 *Tables*

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By G. U. Gitmez & W. A. S. Sarjeant

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I. INTRODUCTION

THIS paper contains an account of assemblages of organic-walled microplankton (dinoflagellates and acritarchs) from the Kimmeridgian of England, Scotland and France. Since an account has already been given of assemblages from the lowest Kimmeridgian, the Baylei Zone (Gitmez, 1970), attention is concentrated on the higher zones: however, additional records from the Baylei Zone are included and data respecting this zone is incorporated into the stratigraphical discussion.

Many of the samples examined were collected by the second author (W.A.S.S.), with the help or under the guidance of a number of other geologists—in Dorset, from Dr. J. C. W. Cope (University of Wales, Swansea); in the French Jura and the Boulonnais, from Professor Derek V. Ager (then of Imperial College, London; now of the University of Wales, Swansea); in Normandy and Le Havre, from Dr. Michel

Rioult (Université de Caen); in Lorraine, from M. Pierre L. Maubeuge; and in Skye, from Dr. Dennis Field (University of Nottingham). In addition, a series of samples from the Warlingham borehole of H.M. Geological Survey were made available for study, through the courtesy of the Director, Dr. F. W. Anderson and Dr. H. Ivimey-Cook; and samples from Cromarty and from Oxfordshire and Cambridgeshire were furnished respectively by Dr. W. D. Ian Rolfe (Hunterian Museum, University of Glasgow) and Dr. Robin I. Whatley (University of Wales, Aberystwyth).

Preparation and preliminary study of the samples was done by the first author (G.U.G.), who also prepared most of the diagrams and photographs. The results were worked out jointly. It was found that many species were represented by insufficient individuals for satisfactory description; repreparation and further study of the samples were therefore to have been undertaken. This was precluded by the destruction by fire of the upper floor of the Geology building of the University of Nottingham in late March, 1970; all wet and dry samples and many microscope slides were lost and the research programme of the second author (W.A.S.S.) so seriously set back that further work on the Kimmeridgian cannot now be envisaged for some years to come. In consequence, it was considered that, since so little is known of the assemblages from these levels, the data currently available should be published forthwith.

In many instances, samples examined did not yield assemblages; relatively pure limestones in particular proved unproductive, the bulk of the assemblages being obtained from clays or argillaceous limestones. Details are given here of the negative as well as of the positive results.

II. LOCATION AND DESCRIPTION OF SAMPLES

Since full stratigraphic details and sample numbers for the specimens from the Baylei Zone have already been given (Gitmez, 1970), these are summarized only briefly here. Location, position and specimen numbers for higher horizons are given in full. Nottingham University sample numbers are quoted, since these were employed in all notes made by the authors. [The samples themselves were all destroyed in the conflagration.]

The history of the ammonite zonation proposed for the Kimmeridgian of England is outlined in Table 1. The zonation here adopted is based on that of Arkell (1956) and incorporates the modifications introduced by Cope (1967).

(1) Dorset (South coast):

The clay formation known as the Kimmeridge Clay represents long-continued deposition of muddy sediments. It is not a uniform deposit, for it includes several lithological types which may alternate in rapid succession; in addition to thick clays there are thin bands of mudstone and several prominent "stone-bands", formed by limestones of variable degrees of purity (see Arkell, 1933; Cope, 1967).

The Kimmeridge Clay is well exposed on the Dorset coast, through faulting in Ringstead Bay and again near Osmington Mills which causes repetition of the succession. Around the type locality of Kimmeridge, the Kimmeridge Clay reaches its maximum thickness (495 m), but towards the west, in the Weymouth district, the thickness is nearly halved and inland it reduces to 90 m.

TABLE I

The history of the zonal classification of the Kimmeridgian

Oppel 1856–1858	Salfeld 1913–1914	Neaverson 1925	Arkell 1956	Arkell 1956, modified after Cope 1967	Major Units
PORTLANDIAN					
	(Pavlovia pallasioides) (Pavlovia pallasianus) (Pavlovia rotunda)	Pavlovia pallasioides	Pavlovia pallasioides	Pavlovia pallasioides	UPPER
		Pavlovia rotunda	Pavlovia rotunda	Pavlovia rotunda	
	Pectinatites pectinatus	Pectinatites pectinatus	Pectinatites pectinatus	Pectinatites pectinatus	
	Virgatites miatschkovensis	Virgatosphinctoides nodiferus	Subplanites wheatleyensis	Pectinatites (Arkellites) hudlestoni	
		Virgatosphinctoides wheatleyensis	Subplanites grandis	Pectinatites (Virgatosphinctoides) wheatleyensis	MIDDLE
			Subplanites spp.	Pectinatites (Virgatosphinctoides) scitulus	
Steraspis	Gravesia irius	Gravesia Zones	Gravesia gigas	Pectinatites (Virgatosphinctoides) elegans	
	Gravesia gravesiana		Gravesia gravesiana		
"Mutabilis"	Aulacostephanus pseudomutabilis	Aulacostephanus pseudomutabilis	Aulacostephanus pseudomutabilis	Aulacostephanus autissiodorensis	
				Aulacostephanus eudoxus	LOWER
	Rasenia mutabilis	Rasenia mutabilis	Rasenia mutabilis	Aulacostephanoides mutabilis	
Tenuilobatus	Rasenia cymodoce	Rasenia cymodoce	Rasenia cymodoce	Rasenia cymodoce	
	Pictonia baylei	Pictonia baylei	Pictonia baylei	Pictonia baylei	
OXFORDIAN					

The samples studied were collected from two areas, the Isle of Purbeck and the Weymouth district (Text-fig. 1). Fourteen samples were examined from the Isle of Purbeck. (The colours are given according to the "Rock Colour Chart", produced by the Geological Society of America [1963] and based on the Munsell System.)

Autissiodorensis Zone:

1. KD 221—Shale containing shell fragments, medium grey in colour (N5), from c. 4 ft above Washing Ledge Stone Band, Kimmeridge (National Grid Reference: 909791).

2. KD 224—Clay containing shell fragments, medium dark grey in colour (N4), from 30 ft above Maple Ledge Stone Band, Kimmeridge. (National Grid Reference: 909788.) [Very few microfossils were obtained from this sample.]

3. KD 225—Clay containing shell fragments, medium dark grey in colour (N4), from immediately below the cementstone at the junction of the Autissiodorensis and Elegans Zones, Kimmeridge. (National Grid Reference: 909789.)

Elegans Zone:

4. KD 227—Clay containing shell fragments, medium dark grey in colour (N4), from 25 ft below the Yellow Ledge Stone Band, Kimmeridge. (National Grid Reference: 917780.) [This sample contains few microfossils.]

Scitulus Zone:

5. CD 229—Clay, brownish grey in colour (5 YR 4/1), from 6 ft below the Cattle Ledge Stone Band, Cuddle. (National Grid Reference: 917780).

Wheatleyensis Zone:

6. CH 231—Clay, medium grey in colour (N5), from 22 ft below the Black Stone, Clavells Hard. (National Grid Reference: 920778.)

7. RD 234—Clay, medium grey in colour (N4), from 13 ft above the Rope Lake Head Stone Band, Rope Lake Head. (National grid reference: 934785.) [No assemblage was obtained from this sample.]

Boundary of Pectinatus-Hudlestoni Zones:

8. FD 236—Marl, medium dark grey in colour (N4), from ¼ mile west of Freshwater Steps, (National grid reference: 946773.)

Pectinatus Zone:

9. FD 237—Marl, containing shell fragments, medium dark grey in colour (N4), from 2 ft above the Freshwater Steps Stone Band, ¼ mile west of Freshwater Steps. (National grid reference: 946773.)

10. ED 240—Marl containing shell fragments, medium grey in colour (N5), from 30 ft above the Freshwater Steps Stone Band, Egmont Bight. (National Grid reference: 948772).

11. ED 242—Clay, medium dark grey in colour (N4), from 60 ft above Freshwater Steps Stone Band, Egmont Bight. (National grid reference: 948772).

12. HC 243—Clay, medium dark grey in colour (N4), from c. 100 ft below the Rotunda Nodules, in the base of Hounstout Cliff. (National grid reference: 951773).

Rotunda Zone:

13. CP 245—Clay containing shell fragments, medium light grey in colour (N6), from the Rotunda Nodule Bed, Chapmans Pool. (National Grid Reference: 956772).

14. HC 246—Clay, medium grey in colour (N5), from 140 ft below the Massive

Bed, Hounstout cliff (National grid reference: 950774). [Few specimens were obtained from this sample.]

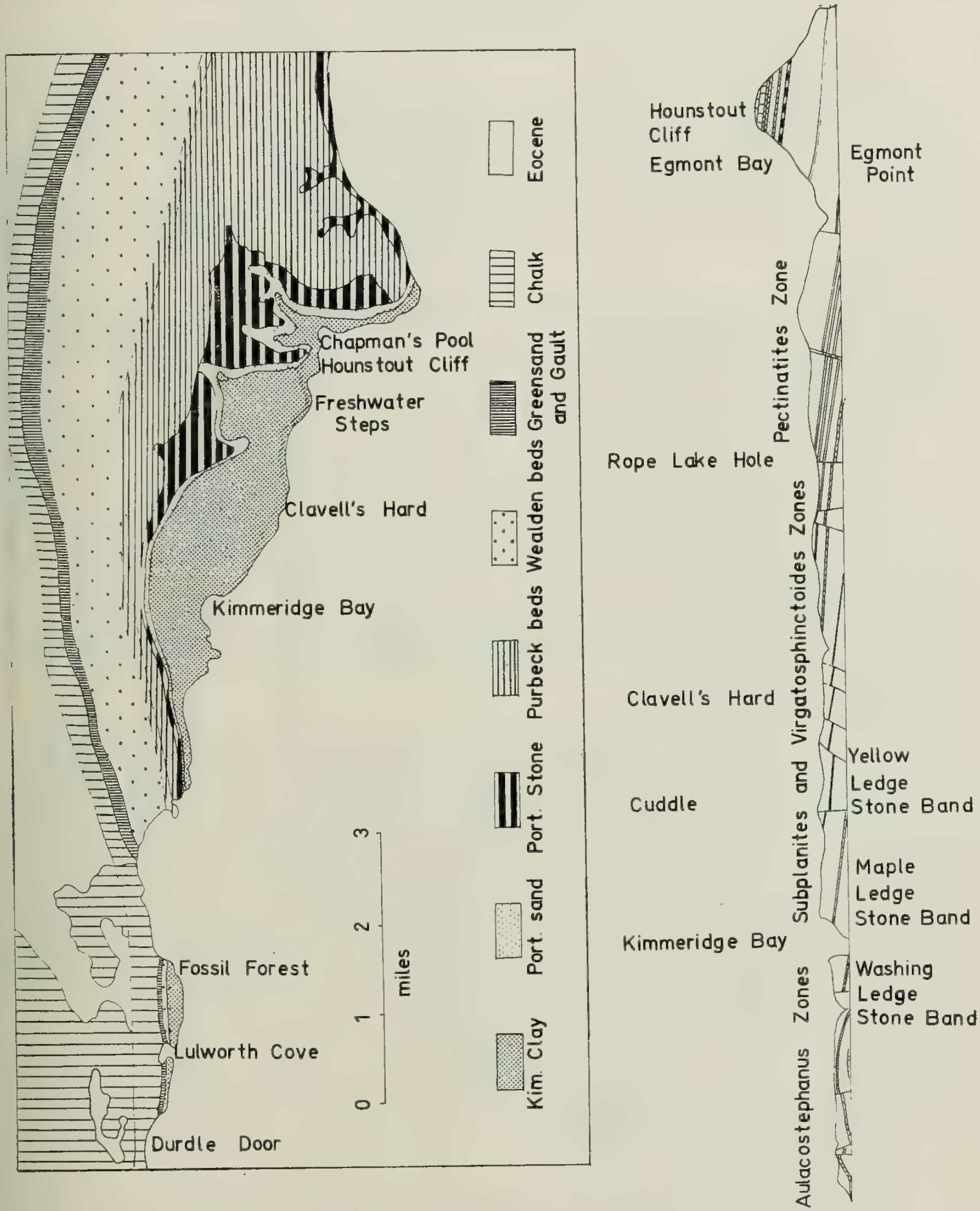
Chapman's Pool
Hounstout Cliff
Freshwater Steps
Clavell's Hard
Kimmeridge Bay
Fossil Forest
Lulworth Cove
Durdle Door
Eocene
Chalk
Greensand and Gault
Wealden beds
Purbeck beds
Port. Stone
Port. sand
Kim. Clay
0
1
2
3
miles
Hounstout Cliff
Egmont Bay
Egmont Point
Pectinatites Zone
Rope Lake Hole
Subplanites and Virgatosphinctoides Zones
Clavell's Hard
Cuddle
Yellow Ledge Stone Band
Maple Ledge Stone Band
Kimmeridge Bay
Washing Ledge Stone Band
Aulacostephanus Zones

FIG. 1. Sketch map of the Isle of Purbeck, showing the positions of the type sections of the Kimmeridge Clay. Section along the cliffs of Kimmeridge Clay (modified from Arkell, 1933).

In the Weymouth District, the Jurassic rocks have been folded and faulted along a N–S line. The Kimmeridge Clay, after a gap, reappears in Ringstead Bay, rising from the sea and partly hidden by slips of Chalk and Greensand. In this part of the Dorset Coast the Kimmeridge Clay is overlying conformably the Ringstead Coral Bed, at the top of the Oxfordian.

Around Osmington Mills, the exposed clay in the cliffs mainly belongs to the Mutabilis and Pseudomutabilis Zones: it is quite deeply weathered and much slipped. The Cymodoce and Baylei Zones, with the Ringstead Coral Bed below, appear from time to time in the foreshore, as a result of periodic stripping of shingle by storms. An account of samples from the Baylei Zone at this locality was given earlier (Gitmez, 1970).

(2) Oxfordshire:

The Kimmeridgian, together with the Portland and Purbeck Beds, occupies a small area, being partially concealed by the overlap of the Cretaceous strata. Three samples from the Pallasioides Zone were examined; these were collected from a quarry at Littleworth, Wheatley (National grid reference: 595055).

1. LO 352—Clay, medium light grey in colour (N6), from 15 ft below the Wheatley Sands.
2. LO 353—Clay, medium grey in colour (N5), from the quarry.
3. LO 360—Clay, light olive grey in colour (5 Y 6/1), from the top of the Kimmeridgian, Littleworth. [No assemblage was obtained from this sample.]

(3) Cambridgeshire:

There are a few exposures of the Kimmeridge Clay in the north west of this area. Only one sample, from the Baylei Zone, was examined from this district: for details see Gitmez, 1970.

(4) Warlingham, Surrey:

The Warlingham borehole was drilled, under contract, in the Geological Survey programme of boring in 1956–1958 and was sited in a field beside the Woldingham Road, Warlingham (National Grid reference: TQ 3476 5719). The boring commenced in Middle Chalk and passed through the Cretaceous and Jurassic rocks, terminating in the Lower Carboniferous at a depth of 5001 ft. At this locality the Kimmeridge Clay is 703 ft thick (between 2284 ft and 2987 ft in depth).

Twenty-nine samples, at 25 ft intervals, from the Rotunda Zone to the Mutabilis Zone, were studied for their organic-shelled microplankton content. These Kimmeridge Clay samples are between light bluish grey and medium bluish grey in colour (5 B 6/1), representing the zones as follows:

Rotunda Zone:

1. WB 29 from 2285′7″ depth.
2. WB 28 ,, 2310′6″ depth.
3. WB 27 ,, 2335′0″ depth.

Pectinatus Zone:

4. WB 26 from 2359′9″ depth.
5. WB 25 ,, 2384′9″ depth. [Few specimens obtained.]
6. WB 24 ,, 2409′9″ depth.

Hudlestoni Zone:
7. WB 23 from 2434′6″ depth.
8. WB 22 ,, 2459′6″ depth. [Few specimens obtained.]
9. WB 21 ,, 2485′0″ depth. [Few specimens obtained.]

Wheatleyensis Zone:
10. WB 20 from 2510′0″ depth.
11. WB 19 ,, 2535′3″ depth.
12. WB 18 ,, 2560′0″ depth.

Scitulus Zone:
13. WB 17 from 2584′9″ depth.
14. WB 16 ,, 2610′0″ depth.

Elegans Zone:
15. WB 15 from 2635′3″ depth.

Autissiodorensis Zone:
16. WB 14 from 2660′1″ depth.
17. WB 13 ,, 2684′3″ depth.
18. WB 12 ,, 2709′3″ depth. [Few specimens obtained.]

Eudoxus Zone:
19. WB 11 from 2734′11″ depth.
20. WB 10 ,, 2760′5″ depth.
21. WB 9 ,, 2785′2″ depth.
22. WB 8 ,, 2810′6″ depth.
23. WB 7 ,, 2834′7″ depth.
24. WB 6 ,, 2860′0″ depth.
25. WB 5 ,, 2885′1″ depth.
26. WB 4 ,, 2910′6″ depth.

Mutabilis Zone:
27. WB 3 from 2935′2″ depth.
28. WB 2 ,, 2959′5″ depth.
29. WB 1 ,, 2984′7″ depth.

(5) Isle of Skye (Staffin Bay):

Three samples were examined from the Baylei Zone of Staffin Bay; these have been fully described by Gitmez, 1970.

(6) Eathie Haven (South of Cromarty):

The Kimmeridgian strata are visible in a narrow shore strip exposed only at low tide. The beds consist of carbonaceous shales, sandstones, bituminous shales and limestones. The total thickness has been calculated as approximately 38 m (Waterston, 1951, p. 33); the apparent thickness is less than the real thickness, because of the displacements consequent upon folding, which render it difficult to determine the thickness accurately (Text-fig. 2 a, b). Only one sample, from the Cymodoce Zone, was examined:

CS 421—Shale, olive black in colour (5 Y 2/1), from the first Meleagrinella Band of Eathie. (National grid reference: 778636.)

(7) The Boulonnais, Pas-de-Calais, France:

The Kimmeridgian rocks are well exposed along the coast of the Boulonnais (see

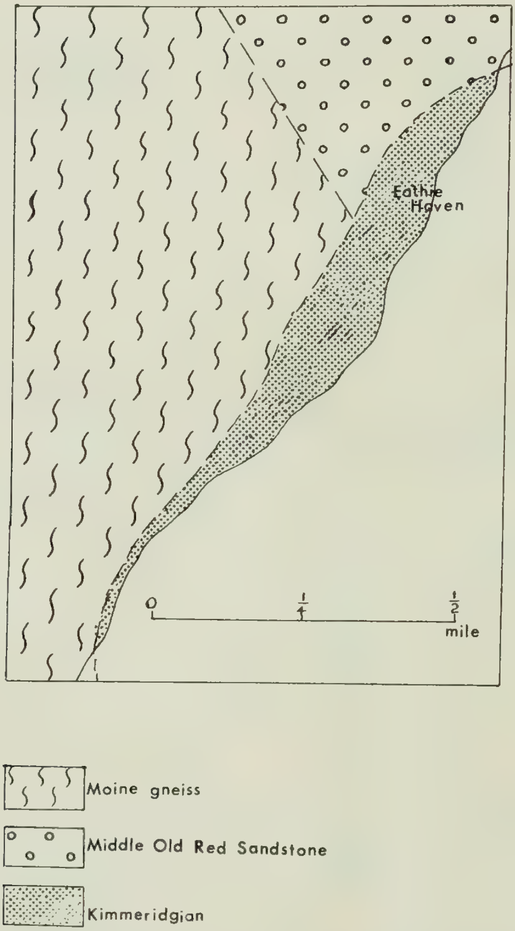

FIG. 2. A. Sketch map showing the geology around Eathie, Cromarty (after Waterston, 1952).

Ager and Wallace, 1966a, b). Eight samples were studied, seven of which (obtained from the basal formations, which are the equivalent of the Baylei Zone in Dorset) were described in a previous paper (Gitmez, 1970). In addition, one was obtained from the Subplanites Zone *sensu* Arkell, here considered probably equivalent to the Scitulus Zone of Cope, 1967.

CC 453—clay, light grey in colour (N7), from Argiles de la Crèche, north of Cap de la Crèche. No microfossils were recovered.

(8) Normandy:

Only the lower Kimmeridgian is represented in Normandy: it appears beneath the unconformable Cretaceous and comprises clays and limestones with ammonites indicative of the Mutabilis, Cymodoce and Baylei Zones. Two samples were studied, one from the Baylei Zone (described by Gitmez, 1970), the other from the Cymodoce Zone:

BN 179—Marls, light olive grey in colour (5 Y 6/1), Benerville, Normandy.

(9) Le Havre, Seine Inférieure:

On the shore at Cap de la Hève, clays and limestones of Kimmeridgian age are exposed, beneath the Cretaceous unconformity, at the foot of the cliffs. Three

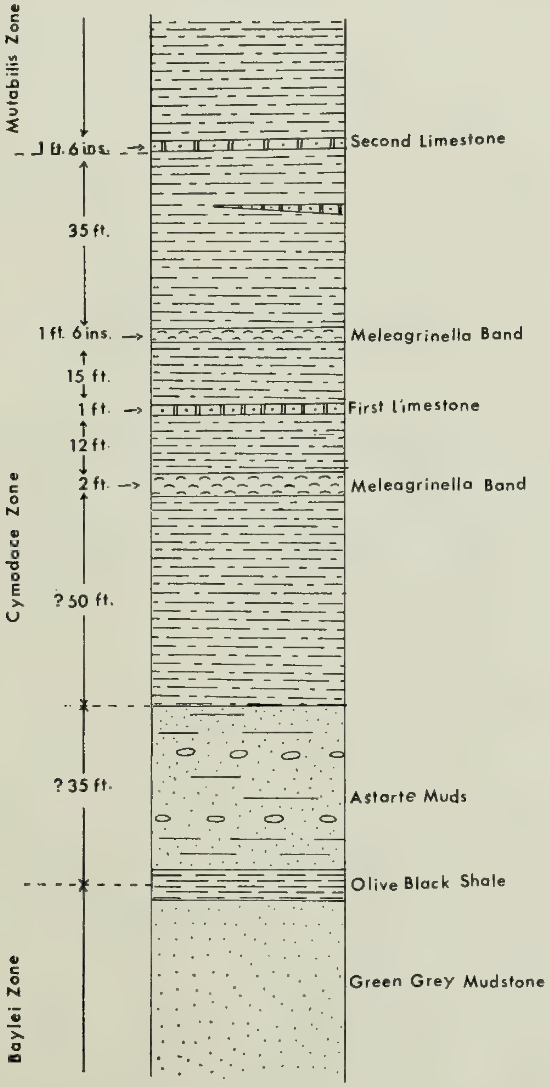
Mutabilis Zone
1 ft. 6 ins.
Second Limestone
35 ft.
1 ft. 6 ins.
Meleagrinella Band
15 ft.
1 ft.
First Limestone
12 ft.
2 ft.
Meleagrinella Band
Cymodoce Zone
? 50 ft.
? 35 ft.
Astarte Muds
Olive Black Shale
Green Grey Mudstone
Baylei Zone

FIG. 2. B. The section of the strata at Eathie, Cromarty (after Waterston, 1952).

samples were studied: two of these, from the Baylei Zone, have already been described (Gitmez 1970); the third sample was from the Mutabilis Zone.

HF 395—Marls, light olive grey in colour (5 Y 6/1), from the Marnes à ammonites, Cap de la Hève.

(10) Lorraine:

In the east of the Paris basin, the Cretaceous usually rests on the Oxfordian; occasionally, however, some Lower Kimmeridgian rocks are still present below the unconformity. Only one sample was obtained from Lorraine:

LF 368—Marl, yellowish grey-light olive grey in colour (5 Y 7/1), collected from the Cymodoce Zone, about 2 ft above the Calcaires à Astartes. Roadside, about 1 km east of Gondrecourt. [This sample contains very few microfossils.]

(11) Mont Crussol (Rhône Valley):

The Jurassic rocks of Mont Crussol comprise a continuous and well-exposed, dominantly calcareous sequence from Upper Bathonian to Tithonian (see Karvé-Corvinus, 1966). The Middle and Lower Tithonian (which is equivalent to the Upper and Middle Kimmeridgian *sensu anglico*) is represented by limestones of various sorts. Thick limestones form the Kimmeridgian stage in its restricted, Continental acceptation (the Tenuilobatus, Pseudomutabilis and Beckeri Zones representing the Lower and Middle Kimmeridgian, *sensu anglico*).

Eight samples were examined, the first sample yielding very few microfossils, the others none at all;

1. MR 547—Limestone, yellowish grey-light olive grey in colour (5 Y 7/1), from the lower boundary of the Platynota Zone (?Baylei Zone), small quarry above the west side of the Ravin d'Enfer.
2. MR 548—Limestone, light grey in colour (N7), from the lower part of the Ataxioceras Zone (Cymodoce-Mutabilis Zones), same locality.
3. MR 549—Limestone, very light grey in colour (N8), from the top of the Ataxioceras Zone, same locality.
4. MR 550—Limestone, pinkish grey in colour (5 YR 8/1), from the *Idoceras balderum* Bed, same locality.
5. MR 552—Limestone, yellowish grey in colour (5 Y 8/1), from the fossil band at the base of Pseudomutabilis Zone (i.e. Autissiodorensis Zone), ridge top above the Carrière Mallet.
6. MR 553—Limestone, yellowish grey-light olive grey in colour (5 Y 7/1), from the Pseudomutabilis Zone, ridge top.
7. MR 554—Limestone, light olive grey in colour (5 Y 6/1), from the lower boundary of the Beckeri Zone (i.e. Autissiodorensis-Elegans Zones), ridge top.
8. MR 555—Limestone, pinkish grey in colour (7 YR 8/1), from the Beckeri Zone, near the summit of the ridge.

(12) The Jura Mountains (Southern French Jura):

As the original type locality for Alexander von Humboldt's "Jurassic", this region is of particular interest. The most important recent work has (rather unexpectedly) been done by English geologists (see Ager and Evamy, 1963). The sequence is again predominantly calcareous and exposure is intermittent but adequate. Three samples from the Oignon Beds and two samples from the Virieu Limestone were examined:

1. OF 485—Limestone (a well-bedded calcilutite), yellowish grey in colour (5 Y 8/1), from the road side, Montard d'Oignon (type locality). Mutabilis Zone.
2. OF 486—Limestone, yellowish-light olive grey in colour (5 Y 7/1), from the top of the Oignon Beds, beneath a pisolite; roadside west of Lac du Chavoley. Mutabilis Zone.
3. OF 487—Pisolitic limestone, yellowish grey in colour (5 Y 8/1), from the junction of Oignon Beds and Bedded Virieu, 2 km north of St. Germain-de-Joux (Mutabilis Zone). [This sample contains few microfossils.]
4. BV 488—Limestone, greenish grey in colour (5 GY 6/1), from the base of Bedded Virieu (Lower Kimmeridgian), calcilutite above pisolite.
5. MV 489—Limestone, pinkish grey in colour (5 YR 8/1), from the Massive Virieu (?Upper Kimmeridgian), 200 yards west of Virieu-le-Grand (type locality). [The sample yielded very few microfossils.]

III. SYSTEMATIC SECTION

Class *DINOPHYCEAE* Pascher

Sub-class *DINOFEROPHYCIDAE* Bergh

Order DINOPHYCIALES Lindemann

Cyst-Family **FROMEACEAE** Sarjeant & Downie, 1966

Genus ***CHYTROEISPHAERIDIA*** Sarjeant, 1962

emend. Downie, Evitt & Sarjeant, 1963

Chytroeisphaeridia chytroides Sarjeant, 1962b

Plate 1, figure 2

1962b *Leiosphaeridia* (*Chytroeisphaeridia*) *chytroeides* Sarjeant, 493–4, pl. 70, figs 13, 16, text-figs 11–12, tables 2–3.
1963 *Chytroeisphaeridia chytroeides* (Sarjeant); Downie, Evitt & Sarjeant, 9.
1964a *Leiosphaeridia chytroeides* Sarjeant; Sarjeant, table 3.
1964 *Chytroeisphaeridia chytroeides* (Sarjeant); Downie & Sarjeant, 103.
1967b *C. chytroeides* (Sarjeant); Sarjeant, table III.
1968 *C. chytroeides* (Sarjeant); Sarjeant, pl. III, fig. 10, table 2B.
1970 *C. chytroeides* (Sarjeant); Gitmez, pl. 14, fig. 5, table 4.
1970 *C. chytroeides* (Sarjeant); Gocht, 152, pl. 34, figs 20–24.

Figured specimen: I.G.S. slide PK102A: Sample WB 2, Kimmeridge Clay. H.M. Geological Survey Borehole, Warlingham, Surrey, at 2959 feet 5 in. depth. Lower Kimmeridgian (Mutabilis Zone).

Dimensions: Figured specimen: length (apex lacking) 45μ, breadth 48μ. Range of the English specimens: length (apex lacking) 12–72μ, breadth 18–80μ, measured specimens 1029 in number. Range of the Scottish specimens (40 specimens measured): length (apex lacking) 20–50μ, breadth 22–75μ. 161 specimens from French assemblages were measured: length (apex lacking) 16–62µ, breadth 22–65µ. There is no significant difference between the size of specimens from different zones in the Kimmeridgian or between English, Scottish and French specimens. The Kimmeridgian specimens exhibit a somewhat wider dimensional range than do the Oxfordian specimens; diameters of the latter, as quoted by Sarjeant (1962b), are 30–60µ.

OBSERVED RANGE: Kimmeridgian (Baylei to Pallasioides).

TOTAL KNOWN RANGE: ?Lower Bathonian: certainly Callovian (Mariae) to Kimmeridgian (Pallasioides).

REMARKS: This species occurs in moderate abundance in all Kimmeridgian assemblages from England, Scotland and France, being most abundant in the Lower Kimmeridgian, numerically somewhat reduced in the Upper Kimmeridgian (Pallasioides Zone).

Chytroeisphaeridia mantelli sp. nov.

Plate 1, figures 3–4; Plate 12, figure 3

DERIVATION OF THE NAME: Named in honour of Gideon Algernon Mantell, pioneer of the study of microplankton.

DIAGNOSIS: Shell subspherical to elongate. The periphragm is coarsely granular and bears an irregular scatter of tubercles and of low knobs, giving it a somewhat warty appearance. An apical archaeopyle is present, with slits extending posteriorly along presumed reflected sutures, producing a ragged appearance. The operculum most often remains attached to the ventral side of the shell.

HOLOTYPE: I.G.S. slide PK116, Sample WB 13, Kimmeridge Clay, H.M. Geological Survey Borehole, Warlingham, Surrey, at 2684 ft 2 in. depth. Lower Kimmeridgian (Autissiodorensis Zone).

PARATYPE A: I.G.S. Slide PK114, Sample WB 13.

PARATYPE B: BM(NH) slide V.56338 (1) sample CH 231, from 22 ft below the Blackstone, Clavells Hard, Dorset. Middle Kimmeridgian (Wheatleyensis Zone).

DIMENSIONS: Holotype: overall length 65µ, breadth 60µ. Paratype A: overall length (apex lacking) 60µ, breadth 65µ. Paratype B: overall length (apex lacking) 65µ, breadth 70µ. Range of Lower Kimmeridgian specimens: length (apex lacking) 25–75µ, breadth 30–65µ, measured specimens 12 in number. Range of Middle Kimmeridgian specimens: length (apex lacking) 40–80µ, breadth 50–75µ, measured specimens 16 in number. Range of Upper Kimmeridgian specimens: length (apex lacking) 23–70µ, breadth 28–75µ, measured specimens 12 in number.

According to these measurements, the species attained its largest size in the Middle Kimmeridgian.

DESCRIPTION: The thick shell wall is apparently composed of two layers: the inner layer thin, the outer layer making up almost the entire wall thickness. The ornamentation of the periphragm is of three types: coarse granules, small irregularly formed lumps (verrucae) and rounded tubercles, irregularly scattered. A tabulation is indicated only by the slits; there is no suggestion of a cingulum. The sulcal notch was seen only in specimens in which the operculum was completely lost; it was not perceptible in specimens with the operculum still attached. This is considered to indicate that when the operculum is present, it is attached to the ventral side of the cyst.

REMARKS: *C. mantelli* differs from previously described species of the genus in its relatively thick wall, the ornamentation of the periphragm and the form of its apical archaeopyle. The most similar species is *C. euteiches* Davey (1969), from the Cenomanian; but the shell wall of this new species is not so thick as in *C. euteiches* (2·3μ as quoted by Davey). Although *C. euteiches* has an apical archaeopyle, it is angular in outline and generally narrower, whereas in *C. mantelli* the archaeopyle is characteristically wide, with deep slits passing posteriorly from its margin. (Davey mentioned that the apical archaeopyle of *C. euteiches* also has small slits extending posteriorly from the margin.)

This new species, in its surface ornamentation and wall structure, also shows a broad accord with the diagnosis of *Tenua* as emended by Sarjeant (1968b). Since cingulum and sulcus are not indicated and since, although the cyst wall shows a considerable ornament, spines are not present, it was allocated to the genus *Chytroeisphaeridia*. However, it should be noted that the form of the archaeopyle is closer to that of *Tenua* than to that of typical species of *Chytroeisphaeridia*. This species is thus intermediate in morphology between the genera *Chytroeisphaeridia* and *Tenua*.

C. mantelli was recorded from all zones of the Kimmeridge Clay; it was more abundant in the Middle Kimmeridgian (Eudoxus to Elegans Zones) than in the other subdivisions of the Kimmeridgian. Thirty-seven specimens from England and five specimens from France were examined; it was not observed in the Scottish assemblages.

Chytroeisphaeridia pococki Sarjeant, 1968

Plate 1, figure 5

1965 *Chytroeisphaeridia* sp. Sarjeant, pl. 1, fig. 13.
1968 *Chytroeisphaeridia pococki* Sarjeant, 230, pl. 3, fig. 9.
1970 *C. pococki* Sarjeant; Gitmez, pl. 9, fig. 7, pl. 10, fig. 3, table 4.

FIGURED SPECIMEN: BM(NH) Slide V.53961(3). Sample SC 444, from Great Ouse River Board Pit, Stretham, Cambridgeshire. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Figured specimen: length (apex lacking) 18μ, breadth 22μ. Range of Lower Kimmeridgian specimens: length (apex lacking) 18–85μ, breadth 22–78μ, measured specimens 178 in number.

Range of Middle Kimmeridgian specimens: length (apex lacking) 35–75μ, breadth 35–80μ, measured specimens 113 in number.

Range of Upper Kimmeridgian specimens: length (apex lacking) 28–80μ, breadth 35–80μ, measured specimens 61 in number.

There is no difference in dimensions between the English, Scottish and French specimens. Lower and Middle Kimmeridgian specimens are of comparable dimensions to those of the Oxfordian holotype (dimensions, as quoted by Sarjeant; length [apex lacking] 45μ, breadth 55μ).

Observed range: Kimmeridgian (Baylei to Pallasioides).

Total known range: Callovian (Lamberti to Mariae) and Kimmeridgian (Baylei to Pallasioides) of Europe; Upper Jurassic of Canada.

Remarks: *C. pococki* is present in the Kimmeridgian assemblages from England, Scotland and France: although present at all levels, it was found to be most abundant in the Lower and Middle Kimmeridgian, being especially common in the Warlingham borehole samples.

Genus ***FROMEA*** Cookson & Eisenack, 1958

Fromea warlinghamensis sp. nov.

Plate 1, figures 6, 8; Plate 9, figures 5–6

Derivation of the name: Named after the type occurrence in the Warlingham borehole, Surrey.

Diagnosis: Cyst broadly ovoidal to almost spherical, with a relatively thick wall. Archeopyle apical, subhexagonal to almost circular; a rather rounded projection, not always observable, appears to be a sulcal tongue. The shell surface is densely and coarsely granular. A cingulum is indicated by indentations at the margins; less frequently, it is traceable across the surface.

Holotype: I.G.S. slide PK115, Sample WB 13, Kimmeridge Clay, H.M. Geological Survey borehole, Warlingham, Surrey, at 2684 ft 3 in. depth. Lower Kimmeridgian (Autissiodorensis Zone). Paratypes (a) BM(NH) slide V.56339(2), sample CH 231, slide V.56339(2) Kimmeridge Clay 22 ft below the Black Stone (Wheatleyensis Zone), Clavell's Hard, Dorset. (b) BM(NH) slide V.56340(1), sample LO 353, top of Kimmeridge Clay (Pallasioides Zone), Littleworth, Oxfordshire.

Dimensions: Holotype: length (apex lacking) 47·3μ, breadth 40·5μ. Paratype (a): length (apex lacking) 81·5μ, breadth 79·5μ. Paratype (b): length (apex lacking) 71μ, breadth 65μ. Range of specimens observed (25 in number); length (apex lacking) 42–95μ, breadth 40–88μ.

Description: The pronounced original sphericity characteristic of this species results in a variety of structures produced by compression; paratype (a) in particular, shows an irregular series of bulges. The granules are of variable size and are characteristically circular; the distinctly polygonal granules on the outbulges on paratype (a) probably result from pressure by mineral grains. The wall appears to be composed of a single layer: it may be as much as 2–3μ in thickness.

Observed range: Kimmeridgian (Autissiodorensis to Pallasioides Zones).

Remarks: This new species is distinguished from *Fromea amphora*, the only other species to date placed in this genus, by its much more spherical shape and coarsely granular surface. The known range of the latter species is Barremian to Albian (Cookson and Eisenack, 1958): the stratigraphic hiatus between the type species and this Upper Jurassic species may well be removed by future studies.

Genus ***TENUA*** Eisenack, 1958c emend. Sarjeant, 1968

Tenua capitata (Cookson & Eisenack, 1960b) comb. nov.

Plate 1, figures 11–12

1960b *Hystrichosphaeridium capitatum* Cookson & Eisenack, 252. pl. 39 fig. 9.
1964 *H. capitatum* Cookson & Eisenack; Sarjeant, table 3.
1964 *H. capitatum* Cookson & Eisenack; Downie & Sarjeant, 120.
1970 *Tenua* cf. *capitata* (Cookson & Eisenack); Gitmez. pl. 10, fig 4. table 4.

DESCRIPTION: Cyst spherical to elongate, with an apical archaeopyle and rounded antapex, bearing processes whose length sometimes reaches to one-third of the shell breadth and which number around fifty. The processes are hollow, capitate or briefly bifurcate, their distribution appearing random.

FIGURED SPECIMEN: BM(NH) slide V.56341(1) sample HF 185, from the Exogyra Marls, c. 1 m above the Upper Hard Band, Cap de la Hève, Le Havre. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Range of the English specimens: length (apex lacking) 30–65μ, breadth 22–50μ (7 specimens measured). Range of the French specimens: length (apex lacking) 30–40μ, breadth 22–33μ (2 specimens measured). 3 specimens from the Scottish assemblages were recorded and measured: length (apex lacking) 30–58μ, breadth 30–58μ. Overall range of process length (all localities) 3–10μ. There is not much difference between these dimensions and the dimensions of the Australian specimens quoted by Cookson and Eisenack (length 64–66μ, breadth 28–44μ, process length 8μ).

OBSERVED RANGE: Kimmeridgian (Baylei to Mutabilis).

TOTAL KNOWN RANGE: Jurassic (Oxfordian to Kimmeridgian).

REMARKS: This species, under the name of *Hystrichosphaeridium capitatum*, has previously been recorded from the Oxfordian to Kimmeridgian of Australia by Cookson and Eisenack. It is transferred to the genus *Tenua* on the basis of shell outline, the presence of an apical archaeopyle, and the form and number of the processes. The processes do not clearly reflect any tabulation.

Well-preserved specimens were observed in moderate numbers in samples from the Lower Kimmeridgian only; nine specimens from the Baylei Zone of England and three specimens from that zone in France; three specimens from the Cymodoce Zone of Scotland; and two specimens from the Mutabilis Zone of England were recorded.

These specimens are similar to that figured by Cookson and Eisenack. Although the number of the processes appears greater than in the Australian specimens, it was not possible to make precise comparisons since the number of processes was not mentioned by Cookson and Eisenack.

Tenua echinata sp. nov.

Plate 1, figures 1, 9

1969 *Tenua* sp. Gitmez, 245–6 pl. 8, fig. 3, text-fig. 3, table 4.

Derivation of the name: Latin, *echinatus*, spiny, prickly; referring to the spiny surface of the shell.

Diagnosis: Cyst spherical, subspherical or broadly ovoidal, covered with spines and looking like a prickly ball. Spines very short, broad-based and conical, uniformly distributed over the whole surface, over 200 in number. There is no indication of tabulation, cingulum or sulcus. Archaeopyle usually present, apical in position; the operculum usually remains attached on one side but is sometimes completely lost.

Holotype: BM(NH) slide V.52796(1). Sample OM 131, from the base of the Kimmeridge Clay, *Liostrea delta* Bed, Osmington Mills, Dorset. Lower Kimmeridgian (Baylei Zone).

Paratype: I.G.S. slide PK.119, sample WB 16, from H.M. Geological Survey borehole, Warlingham, Surrey, at 2610 ft depth. Middle Kimmeridgian (Scitulus Zone).

Dimensions: Holotype: overall length 50μ, breadth 50μ; length without apex 43μ; length of the spines 2μ.

Paratype: overall length 72μ, breadth 60μ; length of the spines 2·5μ.

Overall range of the English specimens (15 specimens measured): length 45–90μ, breadth 40–80μ, length without apex (3 specimens were observed without apex) 43–60μ; length of the spines 1·5–2·5μ.

Dimensions of the single French specimen encountered: length (apex lacking) 38μ, breadth 40μ; length of spines 2μ.

Description: The shell surface is smooth. The apex is typically detached in archaeopyle formation. The margin of the archaeopyle is roughly polygonal, with tears extending from the angles along the presumed lines of a reflected tabulation. When the operculum remains attached on one side, this side is probably the ventral side. The spines appear to be solid.

Observed range: Kimmeridgian (Baylei to Pallasioides Zones). Not recorded to date from the Mutabilis, Autissiodorensis and Elegans Zones.

Remarks: This new species of *Tenua* differs from previously described species of the genus in its characteristic shape and in the nature of its spines. It is an infrequent species: 15 specimens from English assemblages and only a single specimen from France were recorded.

Tenua sp.

Plate 1, figures 7, 10

1970 *Chytroeisphaeridia pococki* Gitmez: pl. 9, fig. 8, table 4.

Description: Shell spheroidal to broadly ovoidal, densely granular. The shell wall may or may not be composed of two layers: if the wall is indeed bipartite, then both layers are thin. The outer wall (periphragm?) bears numerous spines whose character is seen clearly only at the margins, especially around the antapex. The spines are slender and short: the relative length of particular spines is, however, highly variable, median spines being consistently shorter than those of the antapical region. At their tips, the spines are most often knobbed, capitate or briefly bifurcate. The cingulum is faintly indicated by two parallel lines in the equatorial region. An apical archaeopyle is developed, with a scalloped margin suggesting partial reflection of a tabulation.

FIGURED SPECIMEN: BM(NH) slide V.53619(1). Sample SS 627, from 100 ft above the second dolerite sill, Staffin Bay, Skye. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Figured specimen: length (apex lacking): 50μ, breadth 55μ, spine length 2–3μ.

REMARKS: This specimen was mentioned earlier as *Chytroeisphaeridia pococki* by one of the authors (Gitmez, 1970), but later examination by high power phase contrast objective showed the presence of spines and other details which made it clear that this specimen is different from *C. pococki*. The observation was based on a single, fairly well preserved specimen. It is generally similar to *Tenua verrucosa* Sarjeant and *Tenua villersense* Sarjeant; the shape of the spines compares closely with those of *T. villersense*, but they are very short, as in *T. verrucosa*. This may be a representative of an undescribed species intermediate between *T. verrucosa* and *T. villersense*.

Cyst-Family **GONYAULACYSTACEAE** Sarjeant & Downie, 1966

Genus ***CRYPTARCHAEODINIUM*** Deflandre, 1939b emend. Gitmez, 1970

Cryptarchaeodinium calcaratum Deflandre, 1939b emend. Gitmez, 1970

1939b *Cryptarchaeodinium calcaratum* Deflandre, 145, pl. 6, fig. 6.
1941a *C. calcaratum* Deflandre; Deflandre, 19, pl. 5. figs. 7–9; text-figs 9–10.
1962 *C. calcaratum* Deflandre; G. & M. Deflandre, fiche 1908.
1964 *C. calcaratum* Deflandre; Downie & Sarjeant, 104.
1964 *C. calcaratum* Deflandre; Eisenack, 153–4.
1964 *C. calcaratum* Deflandre; Sarjeant, table 2.
1965 *C. calcaratum* Deflandre; Górka, 303, pl. 2, figs 3–5, table 1.
1967b *C. calcaratum* Deflandre; Sarjeant, table IV.
1970 *C. calcaratum* Deflandre; Gitmez, 246–8 pl. 1, figs 1–2, text-fig. 4, table 4.

OBSERVED RANGE: Kimmeridgian (Baylei and Rotunda Zones).

TOTAL KNOWN RANGE: ?Oxfordian to Kimmeridgian (Rotunda).

REMARKS: Deflandre first observed this species in the Kimmeridgian assemblages from Orbagnoux (1939); a fuller diagnosis was given later (1941). In 1965, Górka recorded this species for the first time from Poland, in sediments considered to be of Oxfordian age. She observed the archaeopyle formation (by loss of plate 3″) and determined a tabulation similar to that of the Kimmeridgian specimens, except that she mentioned the presence of a second antapical plate: this plate (2′′′′) was never observed in the Kimmeridgian specimens. According to the measurements quoted by Górka, the Polish specimens from the Oxfordian are larger than the English and French Kimmeridgian specimens, with longer sutural spines. The attribution of these Polish specimens to the species *C. calcaratum* must, all in all, be considered very doubtful.

Cryptarchaeodinium **cf.** ***calcaratum***

Plate 2, figure 3; text-figure 3

Description: Shell spherical, with a small, blunt apical horn and rounded, dome-shaped antapex. Tabulation: 4′, 6′′, 6c, 7′′′, 2p, ?1pv and 1′′′′. Apical plates small; plates 1′ and 3′ form the apical horn. The precingular plates are more or less constant in shape and size, the boundary between plates 5′′ and 6′′ not being clear. Cingulum equatorial, a laevorotatory spiral; cingular plates 3c and 4c are the largest and occupy the dorsal side. The postcingular plates are of variable shape and size: plates 1′′′, 2′′′, and 7′′′ are relatively small and triangular, plate 4′′′ (the largest) is more or less square. Two posterior intercalary plates, 1p and 2p, are present and placed on either side of plate 1pv: the boundary between 1p and 1pv was not clear. Plate 2p is very small. The single antapical plate (1′′′′) is convex and its greatest portion is positioned on the dorsal side of the cyst: this does not seem to be the result of distortion in compression. The sulcus is short, being very wide on the epitract but narrowing on the hypotract. On the plate boundaries, crests of irregularly spinous character rise up: some crest spines are briefly bifurcate. The shell surface is minutely granular. An archaeopyle was not observed.

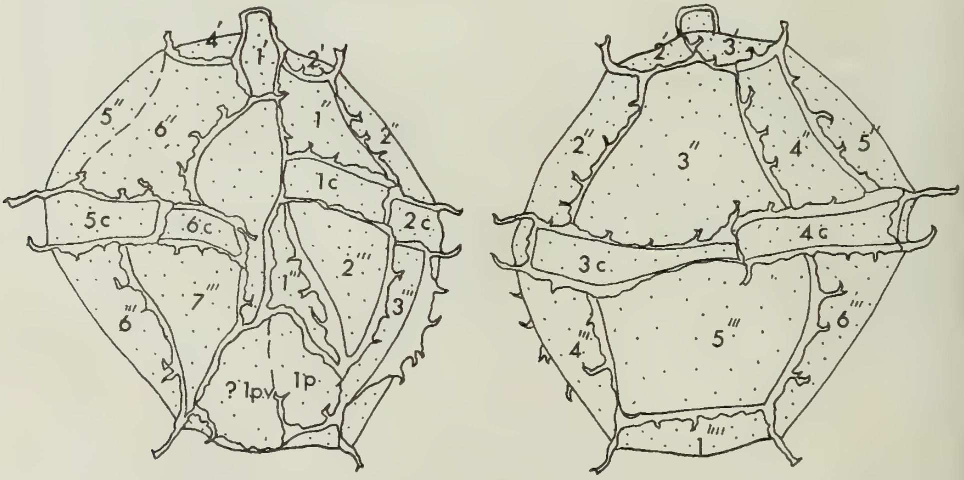

Fig. 3. *Cryptarchaeodinium* cf. *calcaratum* Deflandre. General appearance, showing the tabulation: left, in ventral view; right, in dorsal view. BM(NH) slide V.56342 (1). × c. 1400.

FIGURED SPECIMEN: BM(NH) slide V.56342(1). Sample CS 421, from the first Meleagrinella Band of Eathie, Cromarty. Lower Kimmeridgian (Cymodoce Zone).

DIMENSIONS: Overall length 40–50μ, breadth 35–50μ, horn length 5–6μ, length of the spines on the sutures 4–6μ. Two specimens were measured.

REMARKS: Two specimens observed, one from the Lower Kimmeridgian (Cymodoce Zone) of Scotland and one from the Upper Kimmeridgian (Pectinatus Zone) of Dorset, are similar to *C. calcaratum* except in their possession of an apical horn and in slight differences in the shape of the plates on the hypotract.

Genus ***GONYAULACYSTA*** Deflandre, 1964 emend. Sarjeant, 1969

Gonyaulacysta cauda sp. nov.

Plate 2, figures 1–2, 4–5

1969 *Gonyaulacysta* sp. B Gitmez, pl. 6, fig. 3, text-fig. 14, table 4.

DERIVATION OF THE NAME: Latin, *cauda*, tail, appendage; in reference to the antapical spines.

DIAGNOSIS: The broadly ovoidal cyst possesses a poorly developed apical horn with long spines arising from its tip. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p, 1pv and 1⁗. Spiny crests separate the plates. The single antapical plate is characteristically surrounded by long (nearly three times longer than the other sutural spines), thin, simple spines. Cingulum helicoid, laevorotatory; sulcus moderately broad, extending on both epitract and hypotract to the same length. Surface densely granular. Precingular archaeopyle, if present, formed by loss of plate 3″.

HOLOTYPE: BM(NH) slide V.53965(2) from the sample CC 447, Argiles de Moulin Wibert of Cap de la Crèche, Boulonnais, France. Lower Kimmeridgian (Baylei Zone).

PARATYPE: BM(NH) slide V.56343(1). Sample HC 243, from c. 100 ft below Rotunda Nodules, base of Hounstout Cliff, Dorset. Upper Kimmeridgian (Pectinatus Zone).

DIMENSIONS: Holotype: overall length 78μ, breadth 50μ, apical horn length 8μ; length of the sutural processes 3–5μ, antapical processes 8μ; breadth of the cingulum 3–5μ.

Paratype: length 80μ, breadth 65μ, apical horn length 12μ, antapical processes length 10μ.

A third specimen could not be measured because of its poor preservation.

DESCRIPTION: The slightly helicoid, laevorotatory cingulum of moderate breadth, divides the cyst into two unequal parts. The conical epitract terminates in a poorly developed apical horn, the hypotract is dome-shaped. The epitract is larger than the hypotract, almost two-thirds of the shell length. Apical plate 1′ is elongate, its anterior and posterior ends being narrow; together with plate 3′, it forms the apical horn. Plate 2′ is quite large; 4′ is the smallest of the apical plates. The single anterior intercalary plate 1a is large; as a result plate

6″ is reduced. The precingular plate 1″ is long and narrow; plates 2″, 3″, 4″ and 5″ are large. One of the specimens observed has a precingular archaeopyle, formed by loss of plate 3″. Six postcingular plates occupy the hypotract, together with the single antapical plate and the posterior plates. Plate 1‴ is quadrate and as small as the adjacent sulcal plate; all the other postcingular plates are relatively large. A crescent-shaped plate, 1pv, separates the sulcus from antapical plate 1⁗. The boundary surrounding the antapical plate 1⁗ bears longer spines than the other sutural spines. All the sutural spines are simple, solid, thin, threadlike.

Remarks: This new species is rare, only three specimens being recorded from the following samples: CC 447, RB 219, HC 243 (The first two are from the Baylei Zone, the last from the Pectinatus Zone). It has not been observed in the Middle Kimmeridgian. Two specimens were well preserved, with tabulation and mode of archaeopyle formation easily determinable, but the third was badly preserved. With their long spines distributed like tassels around the antapex, these specimens are different from all previously described proximate dinoflagellate cysts.

***Gonyaulacysta* cf. *giuseppei* (Morgenroth, 1966) Sarjeant, 1969**

Plate 3, figures 3–4, text-figure 4

Description: Cyst subspherical to globular, with the tabulation 4′, 6″, 6c, 6‴, 1p and 1⁗. The cingulum is strongly helicoid, laevorotatory, dividing the cyst into two equal parts: the epitract ends in a short apical horn, the hypotract has a conical aspect with very convex antapex. The apical plates combine to form the

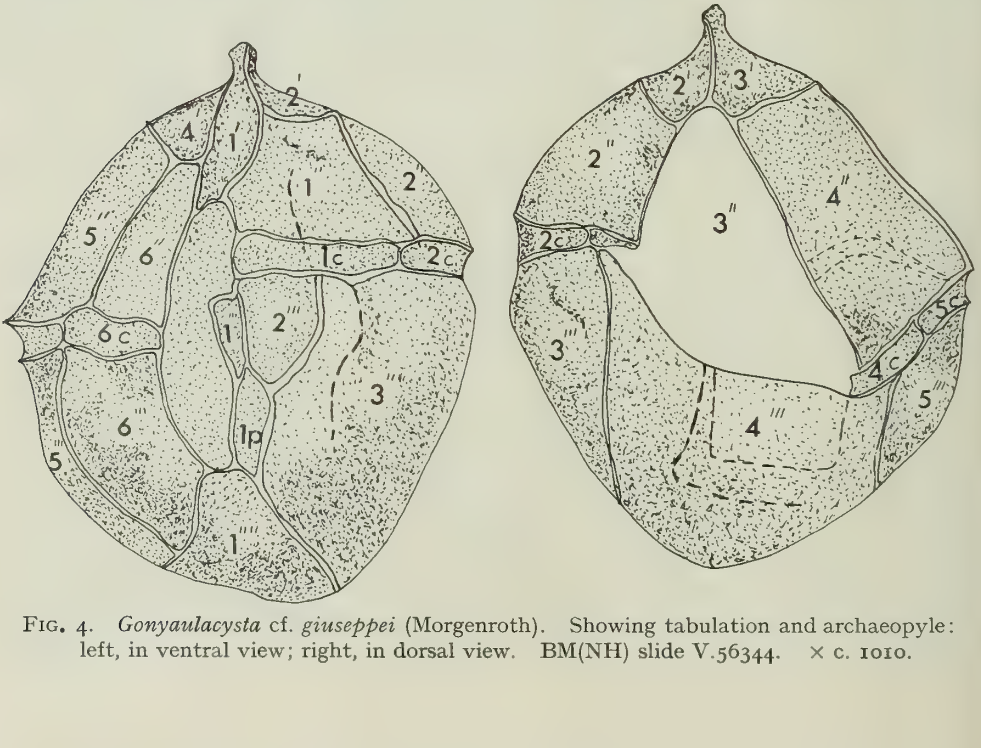

Fig. 4. *Gonyaulacysta* cf. *giuseppei* (Morgenroth). Showing tabulation and archaeopyle: left, in ventral view; right, in dorsal view. BM(NH) slide V.56344. × c. 1010.

apical horn. The precingular plates, except plate 6″, are quite large. Plate 3″ is subtriangular in shape and lost in archaeopyle formation, together with some parts of the cingulum (plate 3, figure 4). The postcingular plates are of variable size and shape: plates 1″ and 2‴ are both reduced to accommodate the long posterior intercalary plate 1p. Plates 3‴ and 4‴ are the largest of all the plates. A single convex plate occupies the antapex. The sulcus is broad, extending between the apex and the antapex. The surface of the shell is granular. Crests on the plate boundaries are low and membraneous.

Figured specimen: BM(NH) slide V.56344(1). Sample CC 448 from Calcaires de Moulin Wibert, south side of Cap de la Crèche, Boulonnais. Lower Kimmeridgian (Baylei Zone).

Dimensions: Figured specimen: overall length 78μ, breadth 62μ, length of apical horn 6μ. Range of the observed specimens: overall length 65–78μ, breadth 58–62μ, horn length 5–6μ. (Measured specimens 4 in number.) Morgenroth gave the following dimensions for *G. giuseppei* (Eocene): length 67–87μ, breadth 67–78μ, horn length 6–8μ. The specimens from the Kimmeridgian are thus slightly smaller than the true *G. giuseppei.*

Remarks: Four specimens from the Lower Kimmeridgian assemblages of the Baylei and Mutabilis Zones (one from France, three from England) are closely similar to *G. giuseppei,* recorded from the Lower Eocene of Germany by Morgenroth (1966). The only major difference is in the shape of the precingular archaeopyle; *G. giuseppei* has a very large, markedly polygonal archaeopyle, but in the Kimmeridgian specimens observed, the archaeopyle is somewhat smaller and tapers so markedly towards the apex that it appears almost triangular. Since the big stratigraphical gap makes it improbable that these specimens are conspecific with *G. giuseppei,* they are compared with, rather than attributed to that species.

Gonyaulacysta globata sp. nov.

Plate 3, figures 1–2; text-figures 5 A–B

Derivation of the name: Latin, *globus,* ball, sphere, in reference to the overall shape of the cyst.

Diagnosis: A proximate cyst, subspherical to broadly ovoidal with a strong apical horn. The sutural crests are low, generally well defined, and reflect the tabulation 4′, 1a, 6″, 6c, 6‴, ?1p and 1⁗. Cingulum moderately narrow, helicoid, laevorotatory, dividing the theca unequally, the epitract being longer than the hypotract. The sulcus is broad. The surface of the shell is densely granular. A precingular archaeopyle, formed by loss of plate 3″, is developed in some instances.

Holotype: I.G.S. slide PK.122, Sample WB 20, H.M. Geological Survey Borehole, Warlingham, Surrey at 2510 ft depth. Middle Kimmeridgian (Wheatleyensis Zone).

Paratype: BM(NH) slide V.56345. Sample FN 236, from the White Stone Band, ¼ m west of Freshwater Steps, Dorset. Middle Kimmeridgian (boundary of Pectinatus-Hudlestoni Zones).

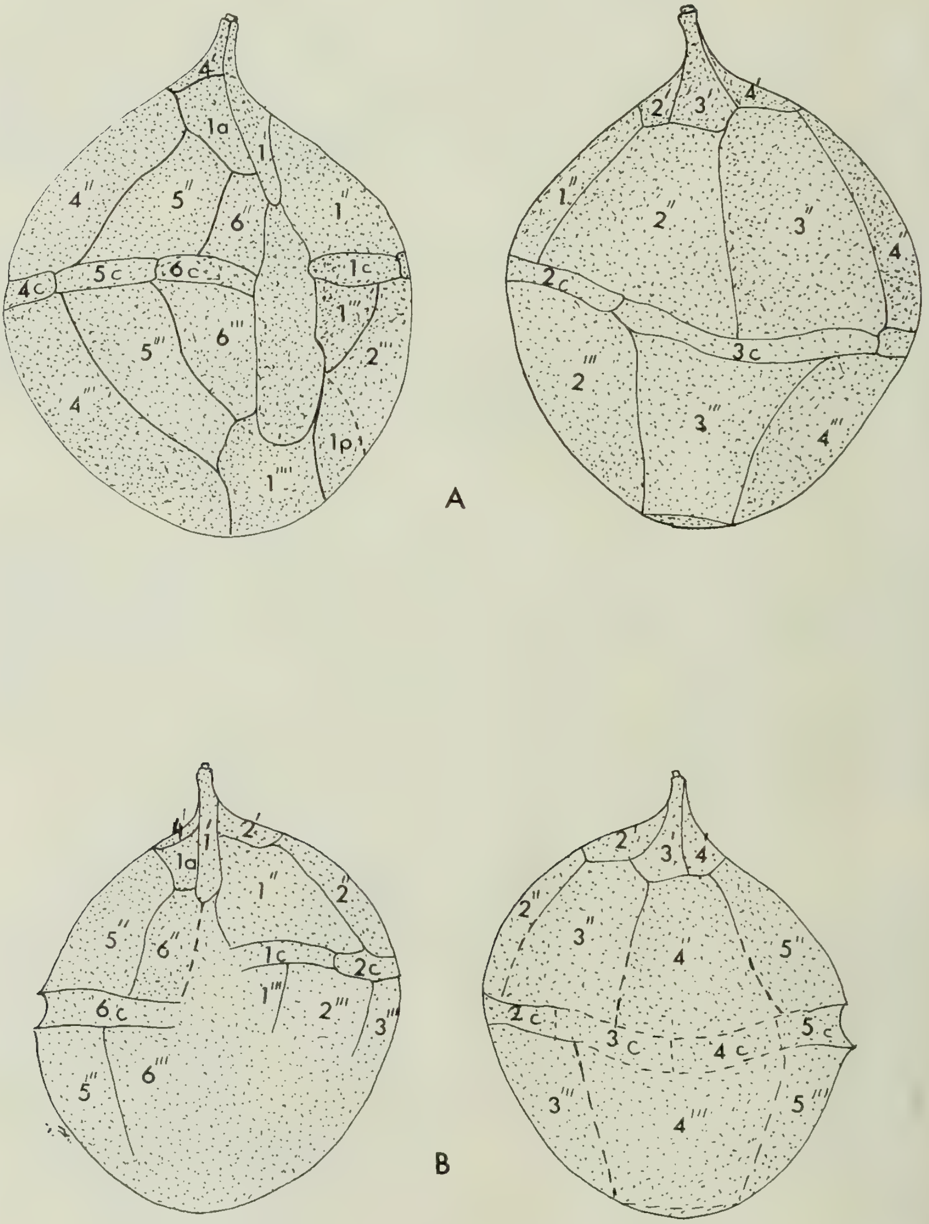
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Fig. 5. *Gonyaulacysta globtaa* sp. nov. A. Holotype: left, in ventral view; right, in dorsal view. I.G.S. slide PK 122. × c.800. B. Paratype: showing the epitractal tabulation: left, in ventral view; right, in dorsal view. BM(NH) slide V.56345. × c.655.

DIMENSIONS: Holotype: overall length 90μ, breadth 68μ, apical horn length 11μ. Paratype: overall length 92μ, breadth 75μ, horn length 12μ. Range of the observed specimens: overall length 85–92μ, breadth 62–75μ, horn length 11–12μ. (Four specimens were measured.)

DESCRIPTION: The cyst is globular, relatively thin-walled. Four apical plates combine to form the slender horn. Plate 1′ is narrow and elongate, the other apical plates are approximately polygonal but with an apical prolongation. A single anterior intercalary plate is present and quite large, apical plate 4′ and precingular plates 5″ and 6″ being correspondingly reduced. The four other precingular plates are large. The cingular plates are poorly defined, but appear to number six.

The hypotract is dome-shaped, composed of large reflected plates; plate 4‴ is the largest of all. Plate 1‴ is greatly reduced; plates 5‴ and 6‴ are relatively small. The boundary between the plates 1p and 2‴ was not confirmed. The single antapical plate, 1⁗, is also large.

The sulcus is narrow in its anterior portion, broadening to contact with the cingulum and thenceforward remaining of constant breadth in its posterior portion. It is relatively short and extends to the antapex.

In one specimen only, a precingular archaeopyle was seen, formed by loss of plate 3″.

OBSERVED RANGE: Kimmeridgian (Wheatleyensis-Pectinatus Zones).

REMARKS: This species is extremely infrequent: of four specimens encountered, the holotype and paratype only are moderately well preserved, the other two being folded, crushed and severely damaged.

In its combination of overall morphology and tabulation *G. globata* differs from previously described species of *Gonyaulacysta*. The most closely similar species is *G. nuciformis*, but *G. globata* differs in having a relatively thin cyst wall and dissimilar ventral antapical tabulation.

Gonyaulacysta longicornis (Downie, 1957) Sarjeant, 1969, emend.

Plate 2, figure 6; Plate 4, figure 1; text-figure 6

1957 *Gonyaulax longicornis* Downie, 420, pl. 20, fig. 8; text-figs 2a–b; table 1.
1962 *G. longicornis* Downie; G. & M. Deflandre, fiche 1830.
1964 *G. longicornis* Downie; Downie & Sarjeant, 115.
1964 *G. longicornis* Downie; Sarjeant, table 2.
1964 *G. longicornis* Downie; Eisenack, 371–2.
1966 *Gonyaulacysta longicornis* (Downie); Sarjeant, *nomen nudum*, 131.
1967b *G. longicornis* (Downie); Sarjeant, *nomen nudum*, table 1.
1967b *Gonyaulax longicornis* Downie; Vozzhennikova, table 12.
1969 *Gonyaulacysta longicornis* (Downie); Sarjeant, 10.
1970 *G. longicornis* (Downie); Gitmez, table 4.

EMENDED DIAGNOSIS: This species of *Gonyaulacysta* is characterized by a very long apical horn (not less than one-third of the whole length). Tabulation: 4′, 6″, 6c, 6‴, 1p and 1⁗. Cingulum slightly helicoid, dividing the cyst unequally: the epitract being longer than the hypotract. On the sutures, short, roughly denticulate crests rise up. Precingular archaeopyle sometimes present and formed by loss of plate 3″. Surface of the shell coarsely granular.

Holotype: C. Downie's collection, Micropalaeontological Laboratory, University of Sheffield, KL 11.15; from the Upper Kimmeridge Clay of Norfolk, England.

Figured specimens: I.G.S. slide PK.120, Sample WB 18, Kimmeridge Clay, H.M. Geological Survey Borehole, Warlingham, Surrey, at 2560 ft depth. Middle Kimmeridgian (Wheatleyensis Zone).

BM(NH) slide V.56346(2). Sample LO 353, from the Littleworth Quarry, Oxfordshire. Upper Kimmeridgian (Pallasioides Zone).

Dimensions: Holotype, as quoted by Downie: overall length 92μ, breadth 58μ, horn length 36μ.

Figured specimen from Warlingham Borehole: overall length 115μ, breadth 75μ, horn length 46μ. Figured specimen from Littleworth: overall length 125μ, breadth 85μ, horn length 40μ.

Range of the specimens from England and France: overall length 80–155μ, breadth 55–100μ, horn length 25–60μ. Measured specimens 34 in number.

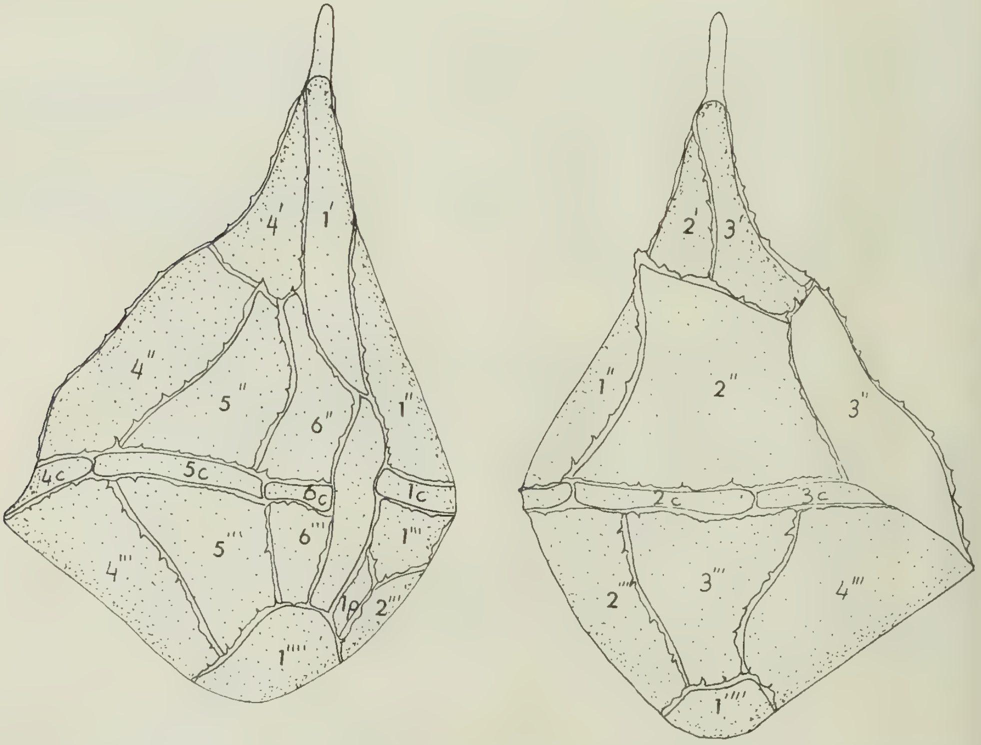

Fig. 6. *Gonyaulacysta longicornis* (Downie). Specimen: left, in ventral view; right, in dorsal view. BM(NH) slide V.56346 (2). × c.704.

DESCRIPTION: The thin-walled shell is roughly polygonal in shape, with a long apical horn and conical hypotract. The apical horn, with its solid tip, is formed by four long apical plates; plate 1′ is elongate, the others are almost triangular. The apical plates, together with six precingular plates, make up the epitract; this is separated from the hypotract by a narrow cingulum and is always longer than the hypotract. Six cingular plates of variable size occupy the cingulum. The sulcus extends onto the epitract and hypotract, between the apex and the antapex. Six postcingular plates of variable shape and size are present: plate 1‴ is reduced to accommodate the posterior intercalary plate, 1p; plates 2‴, 3‴ and 5‴ are more or less uniform in size and plate 4‴ is the largest of all the plates.

OBSERVED RANGE: Kimmeridgian (Baylei to Pallasioides Zones) [See discussion below].

TOTAL KNOWN RANGE: Kimmeridgian (Baylei to Pallasioides Zones).

REMARKS: *G. longicornis* has been known hitherto only from the Upper Kimmeridgian of England. Though the specimens in the French and English assemblages were generally badly preserved, it was possible to determine the tabulation and the mode of archaeopyle formation. This species was doubtfully included in the genus *Gonyaulacysta* by Sarjeant (1969), in the absence of knowledge of the type of archaeopyle; the new observations confirm this reallocation.

The observed specimens are closely similar to Downie's figured specimen, but show slight differences in tabulation. The apical horn is not developed from plate 1′ only, as figured by Downie; instead, it is made up of four apical plates. The posterior intercalary plate was not shown on the figure of the holotype, but was observed in all specimens encountered.

G. longicornis is similar to *Pareodinia nuda* (Downie) in the shape of the apical horn and general appearance; but no tabulation has been yet determined for *P. nuda* and an intercalary archaeopyle was considered by Sarjeant (1967a pp. 254) to be developed in the latter species.

In England, *G. longicornis* was found in most horizons of the Kimmeridgian from Aulacostephanus to Pallasioides, but it was absent from the lowest zones and the Rotunda Zone. In France, in contrast, it was recorded only from the Baylei Zone. Thirteen specimens from France and forty-six specimens from England were recorded.

Gonyaulacysta cf. ***mamillifera*** (Deflandre, 1939b) Sarjeant, 1969

Plate 4, figure 7; text-figure 7

DESCRIPTION: Relatively large, globular shell, broadly ovoidal to subspherical in shape. The more or less equatorial cingulum is slightly helicoid and divides the cyst into two equal parts; the epitract terminates in a mammelon form (in two of the observed specimens, this was well-developed, but the third one has a feebly-developed apical prominence); the hypotract is rounded. Tabulation: 4′, 6″, 6c, 6‴, 1p, 1⁗. Plate boundaries are marked by low membraneous crests. The sulcus is long, extending further on the epitract than on the hypotract; it narrows towards the apex. The shell wall is thin, its surface densely granular and punctate. A precingular archaeopyle is present, formed by the loss of plate 3″.

FIGURED SPECIMEN: I.G.S. slide PK.130, Sample WB 29, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2285 ft 7 in. depth. Upper Kimmeridgian (Rotunda Zone).

DIMENSIONS: Figured specimen: length 92μ, breath 80μ. Range: length 76–92μ, breadth 60–80μ, measured specimens 3 in number. (Holotype dimensions: length 92μ, breadth 84μ, as given by Deflandre).

REMARKS: *G. mamillifera* has only been previously recorded from the Kimmeridgian of France. In this investigation, three specimens probably attributable to this species were observed: one from the Baylei Zone of France and two from the Rotunda Zone of England. In their general aspect they are closely similar to *G. mamillifera*; however, there are differences in the reconstructed tabulation and the ornamentation of the sutures. In the observed specimens the sutures are in the form of membraneous crests, not spinose, as described by Deflandre. The tabulation is generally similar, but the shapes of postcingular plates 1‴ and 2‴ are different. Comparison between the apical plates of this form and *G. mamillifera* was not possible, because Deflandre was unable to determine the apical tabulation. Allocation to this species must, therefore, be provisional only.

Gonyaulacysta nuciformis (Deflandre) Sarjeant, 1969

Plate 3, figure 5; text-figure 8

1938 *Palaeoperidinium nuciforme* Deflandre, 180, pl. 8, figs 4–6.
1962a *P. nuciforme* Deflandre; Sarjeant, pl. 1, fig. 8; tables 3–4.
1962b *Gonyaulax nuciformis* (Deflandre); Sarjeant, 482–3, pl. 69, fig. 6; text-fig. 4; tables 2–3.
1964 *G. nuciformis* (Deflandre); Downie & Sarjeant, 115.
1964 *G. nuciformis* (Deflandre); Sarjeant, table 2.
1964 *Palaeoperidinium nuciformis* Deflandre; Eisenack, 609.
1965 *Palaeoperidinium nuciformoides* Górka, 300–1, pl. 2, figs 1–2; table 1.
1966 *P. nuciformoides* (Deflandre) G. & M. Deflandre, fiche 3030.
1966 ?*Gonyaulacysta nuciformis* (Deflandre); Sarjeant, *nomen nudum* 132.
1967b *Gonyaulax nuciformis* (Deflandre); Vozzhennikova, table 11.
1967b *Gonyaulacysta nuciformis* (Deflandre); Sarjeant, *nomen nudum*, table 1.
1968b *G. nuciformis* (Deflandre); Sarjeant, *nomen nudum*, 227, pl. 3, fig. 4; table 2A.
1969 *G. nuciformis* (Deflandre); Beju, *nomen nudum*, 10, pl. 3, fig. 1; table 1.
1969 *G. nuciformis* (Deflandre); Sarjeant, 10.
1970 *G. nuciformis* (Deflandre); Gitmez, 3, pl. 6, fig. 1; table 4.

DESCRIPTION: The shell is ovoidal to spherical, with the tabulation 4′, 1a, 6″, 6c, 6‴, 1p, 1pv and 1⁗. The epitract and hypotract are more or less equal in size; the epitract ends with an apical horn of variable length, the hypotract is dome-shaped with rounded antapex. The cingulum is helicoid, laevorotatory. The sulcus is broad and extends onto both the epitract and hypotract. The shell is densely granular and relatively thick; because of this, determination of the tabulation is difficult. A precingular archaeopyle was developed by some specimens, formed by loss of plate 3″.

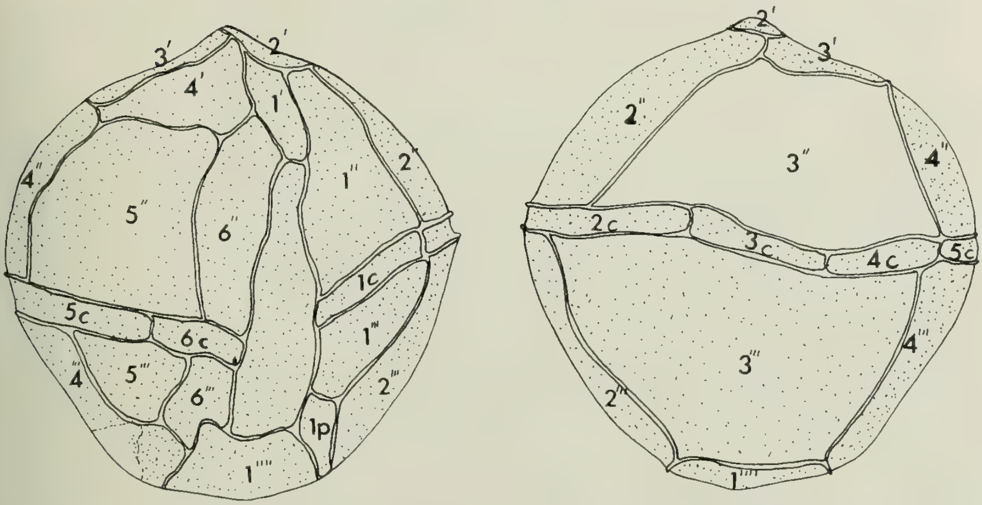
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FIG. 7. *Gonyaulacysta* cf. *mamillifera* (Deflandre). Showing the tabulation: left, in ventral view; right, in dorsal view. I.G.S. slide PK 130. × c.772.

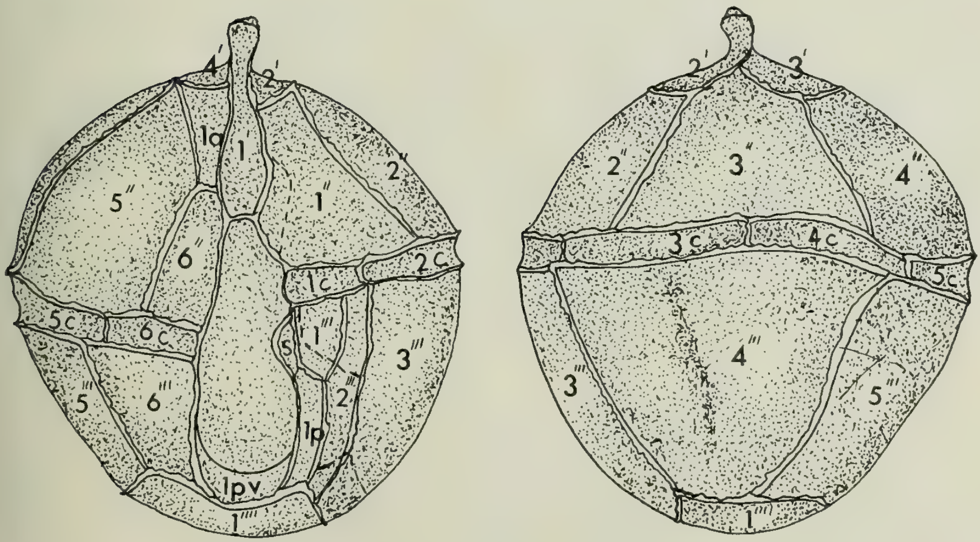
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FIG. 8. *Gonyaulacysta nuciformis* (Deflandre). Tabulation: left, in ventral view; right, in dorsal view. Specimen I.G.S. slide PK 109. × c.1112.

FIGURED SPECIMEN: I.G.S. slide PK.109, Sample WB 7, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2834 ft 7 in. depth. Lower Kimmeridgian (Eudoxus Zone).

DIMENSIONS: Figured specimen: overall length 70μ, breadth 60μ, horn length 9μ.

Range of the Lower Kimmeridgian specimens (61 specimens were measured): overall length 43–118μ, breadth 40–85μ, horn length 4–12μ.

Range of the Middle Kimmeridgian specimens (28 specimens were measured): overall length 68–105μ, breadth 60–85μ, horn length 5–12μ.

Range of the Upper Kimmeridgian specimens (18 specimens were measured): overall length 65–102μ, breadth 55–85μ, horn length 6–12μ.

The following dimensions were quoted by Deflandre for the Oxfordian specimens from France: overall length 60–65μ, breadth 47–53μ (approximately). Dimensions of the Callovian specimens from England, as given by Sarjeant: overall length 56–58μ, breadth 50–64μ. Górka gave the following dimensions for Polish Upper Jurassic specimens: overall length 38–54μ, breadth 40–44μ. Dimensions of the Roumanian specimens (Oxfordian to Kimmeridgian) are given by Beju as overall length 62–78μ, breadth 60–78μ. The Polish specimens are thus smaller than the others and the Roumanian specimens are more spherical. The Kimmeridgian specimens are larger than the specimens from lower stages.

OBSERVED RANGE: Kimmeridgian (Baylei to Pallasioides).

TOTAL KNOWN RANGE: Upper Callovian (Lamberti) to Upper Kimmeridgian (Pallasioides).

REMARKS: *G. nuciformis* was first recorded from the Upper Jurassic of France by Deflandre (1938). Subsequently, this Upper Jurassic species has been observed in several assemblages from Western Europe, and the geographic range has been extended by its observation from the Callovian to Kimmeridgian of Roumania by Beju (1969). It is generally present in moderate abundance in Kimmeridgian assemblages; however, it was not observed in the Middle and Upper Kimmeridgian of France. Also there is a progressive reduction in the number of specimens in the English assemblages through the Upper Kimmeridgian.

The combination *Gonyaulacysta nuciformis* in Beju (1969), although proposed in correct form, was not validly published since a pre-print distributed at a meeting does not constitute effective publication (cf. 'International Code of Botanical Nomenclature', Art. 29). The combination is, therefore, correctly attributed to Sarjeant (1969).

Gonyaulacysta perforans (Cookson & Eisenack) Sarjeant, 1969

Plate 4, figure 6; text-figure 9

1958 *Gonyaulax perforans* Cookson & Eisenack, 30, pl. 2, figs 1–4, 7–8; text-figs 8–9.
1961 *G. perforans* Cookson & Eisenack; Alberti, 6, pl. 11, figs 4–6; tables a–c.
1962 *G. perforans* Cookson & Eisenack; G. & M. Deflandre, fiches 1849–1852.
1963 *G. perforans* Cookson & Eisenack; Balteș, 584, pl. 4, figs 1–6, table 1.
1964 *G. perforans* Cookson & Eisenack; Downie & Sarjeant, 115.

1964 *G. perforans* Cookson & Eisenack; Sarjeant, table 2.
1964 *G. perforans* Cookson & Eisenack; Eisenack, 397–8.
1965 *G. perforans* Cookson & Eisenack; Balteş, 12, pl. 3, figs 93–4.
1966 *Gonyaulacysta perforans* (Cookson & Eisenack); Sarjeant, *nomen nudum*, 131.
1967b *Gonyaulax perforans* Cookson & Eisenack; Vozzhennikova, table 12.
1967 *G. perforans* Cookson & Eisenack; Millioud, pl. 2, fig. 15; text-fig. 1.
1969 *G. perforans* Cookson & Eisenack; Balteş, fig. 3.
1969 *Gonyaulacysta perforans* (Cookson & Eisenack); Sarjeant, 10.

DESCRIPTION: The cyst is elongate, with a long apical horn. The epitract and hypotract are separated by the helicoid, laevorotatory cingulum and are more or less equal in size. Tabulation: 4′, 6″, 6‴, 1p and 1⁗. Plate boundaries are demarcated by membraneous, delicate porate crests, which are well developed around the apex and the antapex. The sulcus is long and narrow, extending from apex to antapex. The shell wall is thin, the surface granular and occasionally perforate. An archaeopyle was rarely observed; when developed, it forms by the loss of plate 3″.

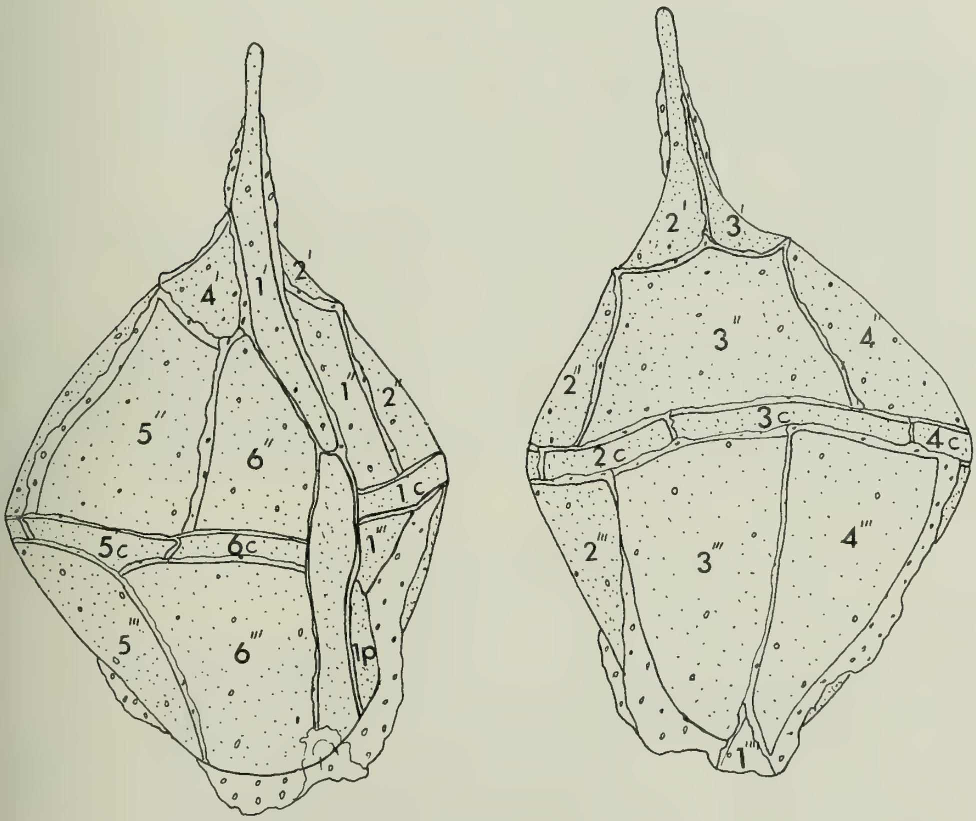


FIG. 9. *Gonyaulacysta perforans* (Cookson & Eisenack). Tabulation: left, in ventral view; right, in dorsal view. I.G.S. slide PK 131. × c.1491.

FIGURED SPECIMEN: I.G.S. slide PK.131, Sample WB 29, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2285 ft 7 in. depth. Upper Kimmeridgian (Rotunda Zone).

DIMENSIONS: Figured specimen: overall length 108μ, breadth 70μ, horn length 33μ. Range of the Middle Kimmeridgian specimens (7 specimens measured): overall length 73–100μ, breadth 54–73μ, horn length 16–18μ. 15 specimens measured from the Upper Kimmeridgian: overall length 80–110μ, breadth 52–75μ, horn length 12–40μ. Cookson and Eisenack gave the following dimensions for the specimens from New Guinea: length 136–168μ, breadth 93–109μ. Dimensions of the specimens from Germany are quoted by Alberti as length 130–145μ and breath 81–103μ. The British and French Middle Kimmeridgian specimens are thus smaller than the Upper Kimmeridgian specimens, but both are smaller than the New Guinea and German specimens.

OBSERVED RANGE: Kimmeridgian (Wheatleyensis to Pallasioides).

TOTAL KNOWN RANGE: Upper Jurassic to Lower Cretaceous (Albian).

REMARKS: *G. perforans* was originally recorded from the Upper Jurassic of New Guinea by Cookson and Eisenack; later Alberti observed it in the Barremian assemblages from Germany and Balteş recorded it from the Albian of Roumania. It is recorded in English assemblages for the first time. The observed specimens are similar to those figured by Cookson and Eisenack, except for small differences in tabulation and in the length of the apical horn.

Although the New Guinea and German specimens are larger than the Kimmeridgian specimens, from the figures they seem to have a proportionately smaller horn. (Since the horn length was not specified, it is possible to deduce this only from the figures.)

Cookson and Eisenack did not mention the presence of apical plate 4′, but in their figure a boundary is shown between the plates 3′ on the ventral side and 3′ on the dorsal side; therefore, the plate on the ventral side should be the fourth apical plate, as observed in the Kimmeridgian specimens. Similarly the elongate plate which they figure below the postcingular plate 1‴ should be the posterior intercalary plate, 1p.

Gonyaulacysta systremmatos sp. nov.

Plate 5, figures 7–8

1970 *Gonyaulacysta* sp. C. Gitmez, 265–7, pl. 4, figures 10–11, text-fig. 15, table 4.

DERIVATION OF NAME: Greek, *systremmatos*, anything consolidated, generally a ball or round object; in reference to the ball-like shape of the shell.

DIAGNOSIS: Thick-walled shell, almost spherical, with a moderately long apical horn. Tabulation: 4′, 1a, 6″, 6–7c, 7‴, 1p, 1pv, 1⁗. The plate boundaries are demarcated by delicate crests of variable height. The cingulum is helicoid, laevorotatory; the sulcus is short and broadens posteriorly. The surface is densely granular. A precingular archeopyle, formed by loss of plate 3″, is generally developed.

HOLOTYPE: BM(NH) slide V.53966(1), from the sample CC 447, Argiles de Moulin Wibert, Cap de la Crèche, Boulonnais, France. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Holotype: overall length 68μ, breath 62μ, horn length 8μ, height of the crests 4–5μ. Range of the observed specimens: overall length 66–78μ, breadth 60–65μ, horn length 7–16μ; measured specimens 5 in number.

DESCRIPTION: The helicoid, laevorotatory cingulum divides the cyst unequally. The epitract is somewhat longer than the hypotract; both are more or less dome-shaped. The number of the cingular plates is hesitantly mentioned, because the character of the small plate beside 6c is doubtful; it may be either a small cingular plate or a short sulcal plate.

Four apical plates make up the apex, plate 1′ occupying the anterior prolongation of the sulcus. Plates 2′ and 3′ are small; plate 4′ is almost as large as plate 1′. The single, small anterior intercalary plate is placed between the plates 4′ and 6″. The precingular plates are generally large, plate 6″ being of reduced size because of the presence of intercalary plate 1a.

The postcingular plates are of variable size and shape: plate 1‴ is very small; plate 2‴ is also reduced and does not have a boundary with the antapical plate. Plates 3‴, 4‴, 5‴ and 6‴ are relatively large; plate 7‴ is in contrast reduced, having nearly the same size as plate 2‴. The quite broad intercalary plate, 1pv, separates the sulcus from the single antapical plate 1⁗.

REMARKS: This is an infrequent species, six specimens being encountered, all from the Baylei Zone of France. They were badly preserved, being somewhat crushed, folded or covered by debris; the holotype was the best oriented for study. In its general form, this new species of *Gonyaulacysta* differs from all described species. The most closely comparable species is *G. palla* Sarjeant, which has a similarly spherical shape and comparable tabulation; but *G. systemmatos* differs in its apical horn, sutural crests, absence of plate 1a, and presence of plate 1pv. In the possession of a seventh postcingular plate, it is comparable with *G. fetchamensis* and *G. ehrenbergii*, but it is markedly different in overall morphology from both these species.

Gonyaulacysta sp. A

Plate 9, figures 1–2

1970 *Gonyaulacysta* sp. A. Gitmez, 263–4, pl. 3, fig. 3, text-fig. 13.

FIGURED SPECIMEN: BM(NH) slide V.56347(2), Kimmeridge Clay (Pectinatus Zone) 60 ft above Freshwater Steps Stone Band, Egmont Bight, Dorset.

DIMENSIONS: Figured specimen: overall length 103μ, length of apical horn 32μ, overall breadth 66·5μ, length of crest spines c. 1·5–2μ.

REMARKS: This form was originally described on the basis of two specimens from the lowest Kimmeridge Clay (Baylei Zone) of Normandy. The discovery of a third specimen at a higher horizon is thus of interest: its dimensions are markedly larger than those of the specimens described earlier (overall length 65μ, breadth 42μ) but its proportions are similar. Yet further specimens of this type must be located before nomenclatural proposals can justly be made.

Gonyaulacysta sp. B

Plate 4, figures 2–3, text-figure 10

Description: Only one specimen of this species has so far been observed. It possesses a subspherical cyst, bearing a moderately well developed apical horn. The strongly helicoid, laevorotatory cingulum divides the cyst into two more or less equal parts: the hypotract is somewhat flattened at the antapex. The sulcus is sigmoidal and narrow. Tabulation: 4′, 6″, 6c, 5‴, 1p, ?1pv and 1⁗.

The apical plates 1′ and 4′ are small and elongate; together with plates 2′ and 3′, they form the apical horn. The precingular plates are quite large. Plate 3″ is lost in archaeopyle formation. On the hypotract, crests demarcate five postcingular plates. Plate 1‴ and 5‴ are reduced because of the presence of posterior plates, but the other postcingular plates are large. A single antapical plate occupies the antapex.

The wall is moderately thin, its surface finely granular and in part tuberculate. Crests on the plate boundaries are delicate; the denticulation is very deep, virtually giving the crests the appearance of a row of bifid spines.

Figured specimen: I.G.S. slide PK.117, Slide WB 15, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2635 ft 3 in. depth. Middle Kimmeridgian (Elegans Zone).

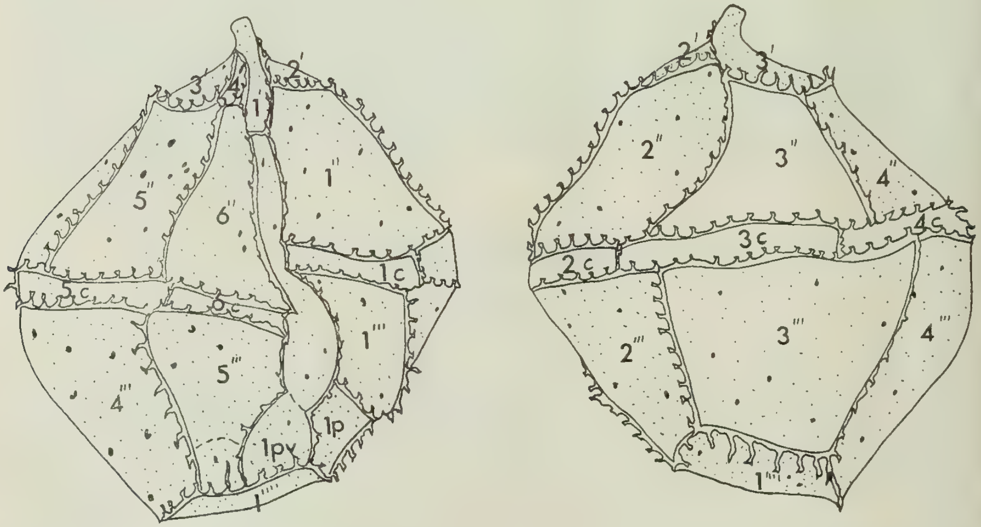


Fig. 10. *Gonyaulacysta* sp. B. Tabulation: left, in ventral view; right in dorsal view. Specimen I.G.S. slide PK 117. × c.1351.

DIMENSIONS: Overall length 48μ, breadth 45μ, horn length 5μ, sutures 3–5μ high.

REMARKS: In its general morphological features and sutural characteristics, this species may be distinguished from all previously described species of *Gonyaulacysta*. The shape of the shell and crests is most comparable to *G. serrata* Cookson & Eisenack (1958) suggesting a relationship between the two species, but the form of the apical horn is different; since a tabulation could not be determined for *G. serrata*, a detailed comparison of these two species is impossible.

Gonyaulacysta sp. C

Plate 6, figures 1–2, text-figure 11

DESCRIPTION: The cyst is subspherical, bearing a short, tapering apical horn. The thickness of the wall is uneven because of irregularly distributed granules. The sutural crests are in the form of low ridges giving rise occasionally to delicate membranes: they indicate a reflected tabulation of 4', 1a, 6'', 6c, 6''', ?1pv, 1''''. Four apical plates together form the horn; plate 1' is elongate in shape. The precingular plates, except plate 6'', are of almost uniform shape and size; plate 6'' is reduced to accommodate the intercalary plate 1a.

Six cingular plates make up the slightly helicoid, laevorotatory cingulum: plate 6c is very small, the others are relatively large. The ends of the cingulum are widely separated by a very broad sulcus, which further widens in its posterior portion.

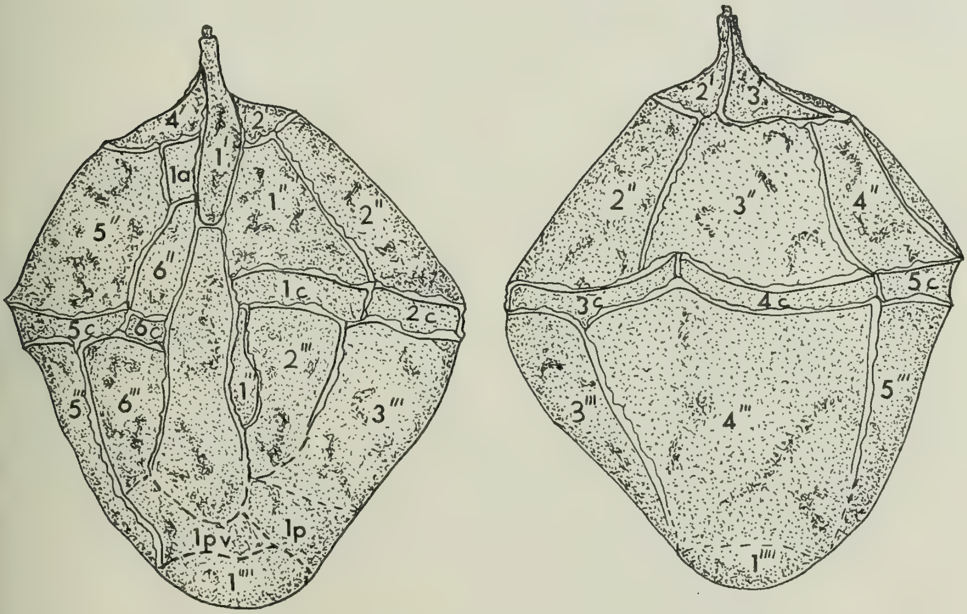


FIG. 11. *Gonyaulacysta* sp. C. Tabulation: left, in ventral view; right, in dorsal view. Specimen I.G.S. slide PK 118. × c.984.

(The antapical end of the sulcus and the plate boundaries near to the antapex were not very clear because of bad preservation of this part of the cyst.) The first post-cingular plate, 1‴, is narrow, elongate and small. Plate 4‴ appears the largest of the post-cingular plates. No archaeopyle was observed in this specimen.

FIGURED SPECIMEN: I.G.S. slide PK.118, Sample WB 16, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2510 ft depth. Middle Kimmeridgian (Scitulus Zone).

DIMENSIONS: Overall length 77μ, breadth 60μ, apical horn length 8μ.

REMARKS: Only one specimen has so far been observed. It is distinguished from all previously described species in its overall morphological features; it is possibly a new species, but further specimens are needed to decide this.

Gonyaulacysta sp. D

Plate 6, figures 4–5; text-figure 12

DESCRIPTION: A specimen with an almost spherical cyst and short, blunt, tapering apical horn. The shell wall is composed of two layers, periphragm and endophragm, which are of the same thickness; the periphragm is coarsely granular. The apical horn is formed of both shell layers. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p and 1⁗. Plate 1′ is elongate and occupies the anterior prolongation of the sulcus. Plates 2′ and 3′ are large; plate 4′ is slightly reduced to accommodate the anterior intercalary plate, 1a. Four apical plates together make up the apical horn. Plate 1a is quite large; because of this, plate 6″ is reduced. The other precingular plates are of more or less similar shape and size. The cingulum is of moderate breath,

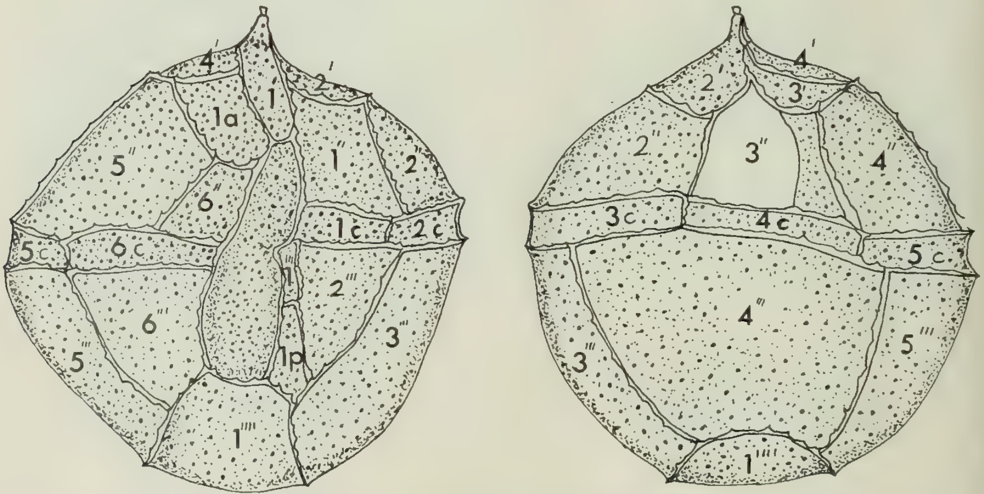


FIG. 12. *Gonyaulacysta* sp. D. Tabulation and archaeopyle formation, Plate 3″ is partially lost in the archaeopyle formation. Specimen BM(NH) slide V.56346 (4). × c.1035.

possessing six cingular plates: plate 1c is smaller and broader than the other cingular plates. Postcingular plate 1‴ is very small and gives the appearance of hanging onto one corner of the cingulum. Plate 2‴ and 6‴ are relatively small; plates 3‴, 4‴ and 5‴ are large. An elongate posterior intercalary plate (1p) is placed below plate 1‴. The single antapical plate, 1⁗, is large and convex. The broad sulcus extends between the apex and antapex.

Plate boundaries are demarcated by low crests and generally well defined. A precingular archaeopyle was seen in some specimens; it forms by loss of plate 3″ (in the figured specimen, plate 3″ is partially detached).

Figured specimen: BM(NH) slide V.56346(4). Sample LO 353, from the Littleworth Quarry, Oxfordshire. Upper Kimmeridgian (Pallasioides Zone).

Dimensions: Figured specimen: overall length 65μ, breadth 60μ, horn length 5μ. Range: overall length 65–80μ, breadth 60–75μ, horn length 4–7μ. Measured specimens 5 in number; 3 other observed specimens could not be measured because of bad preservation.

Remarks: This unnamed species of *Gonyaulacysta* differs from all described species in its general aspect and peculiar apical horn. The most comparable species is *G. palla* Sarjeant, both species having similarly spherical cysts and tapering apical horns. In *Gonyaulacysta* sp. C, the apical horn is broad based and short and its tip appears conical: although *G. palla* has a tapering horn, it is slender and relatively long. The number of the plates on the epitract is the same for both species, but plate 4′ is not placed at the top of the horn as in *G. palla*. The hypotractal plates (especially plates 1‴, 2‴ and 1p) appear similar in shape to those of *G. palla*, but their number is different: *G. palla* has seven postcingular plates, whereas this species has six. The crests of *G. palla* are spiny. The similarity between these two species is thus only in the overall shape.

Eight specimens, all from the same quarry in Littleworth, were recorded; unfortunately, all the specimens encountered are somewhat crushed, folded or covered by debris, which makes them difficult to examine in detail. The figured specimen was the best oriented for study. It may be a new species, but needs further, better preserved specimens for typification.

Gonyaulacysta sp. E

Plate 6, figure 9; text-figure 13

Description: Only one moderately well preserved specimen of this type was observed, in the Lower Kimmeridgian assemblages from the Warlingham Borehole. It possesses an elongate cyst, with conical epitract and dome-shaped hypotract, thus looking rather like a pear. The apical horn is slender and tapering. The wall is densely granular. Plate boundaries are well defined by moderately high membraneous crests. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p, 1pv and 1⁗. Plate 1′ is characteristically long and broad, extending down almost two-thirds of the epitract. Plates 2′ and 3′ are similar to each other; plate 4′ is greatly reduced because of the anterior intercalary plate 1a. For the same reason, plates 5″ and 6″ are also reduced.

The other precingular plates are quite large. The six postcingular plates are of variable shape and size. Plate 1‴ is small and triangular; plates 2‴ and 6‴ are moderately large; plates 3‴, 4‴ and 5‴ very large, together almost occupying the whole dorsal side of the hypotract. A single plate occupies the antapex. The posterior intercalary plate (1p) is elongate. A crescent-shaped plate, 1pv, separates the sulcus from the antapical plate 1⁗. The cingulum is deep, formed by 6 cingular plates, of which 5c and 6c are quite small; it is almost circular and divides the cyst into two unequal parts, with the epitract twice as long as the hypotract. The sulcus is very short and broad. An archaeopyle was not observed.

Figured specimen: I.G.S. slide PK.1113. Sample WB 13, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2684 ft 3 in. depth. Lower Kimmeridgian (Autissiodorensis Zone).

Dimensions: Figured specimen: overall length 65μ, breadth 50μ, apical horn length 7·5μ.

Remarks: The long epitract, densely granular shell wall, elongate apical plate 1′ and large postcingular plates 4‴ and 5‴ distinguish this form from all described species. It almost certainly represents an undescribed species of *Gonyaulacysta*, but before this can be decided, more specimens must be awaited.

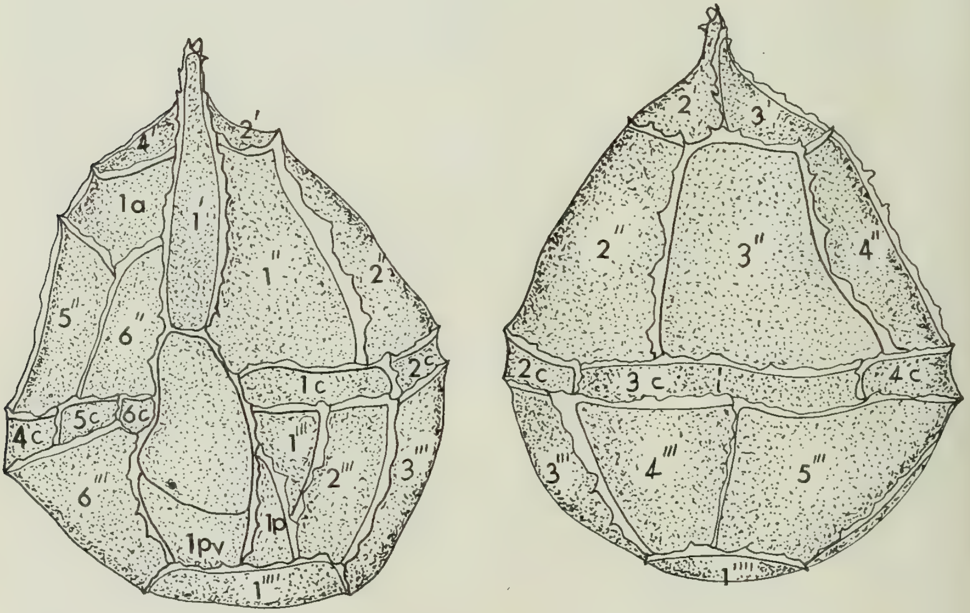


Fig. 13. *Gonyaulacysta* sp. E. Tabulation: left, in ventral view; right in dorsal view. Specimen I.G.S. slide PK 113. × c.669.

Gonyaulacysta sp. F.

Plate 6, figures 3, 6; text-figure 14

Description: The cyst is elongate, with a long and tapering apical horn. The cyst wall is composed of two layers; a fairly thin endophragm and a thicker periphragm. The endophragm bulges into the lower half of the apical horn; the anterior portion of the horn is formed by the periphragm only, so that there is a cavity between the wall layers at the anterior end of the horn. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p, 1pv and 1⁗. The four apical plates together make up the apical horn. Plate 1′ is elongate, extending down two-thirds of the epitract. The anterior intercalary plate (1a) is quite large: because of this, precingular plate 6″ is reduced. The other precingular plates are relatively large. The postcingular plates 1‴ and 6‴ are small, the others are moderately large. The posterior intercalary plate (1p) is elongate: the boundary between the sulcus and the posterior ventral plate (1pv) was not confirmed. A single narrow plate occupies the antapex.

The cingulum is strongly helicoid, laevorotatory, dividing the cyst unequally, the epitract being longer than the hypotract. The sulcus is broad and largely confined to the hypotract.

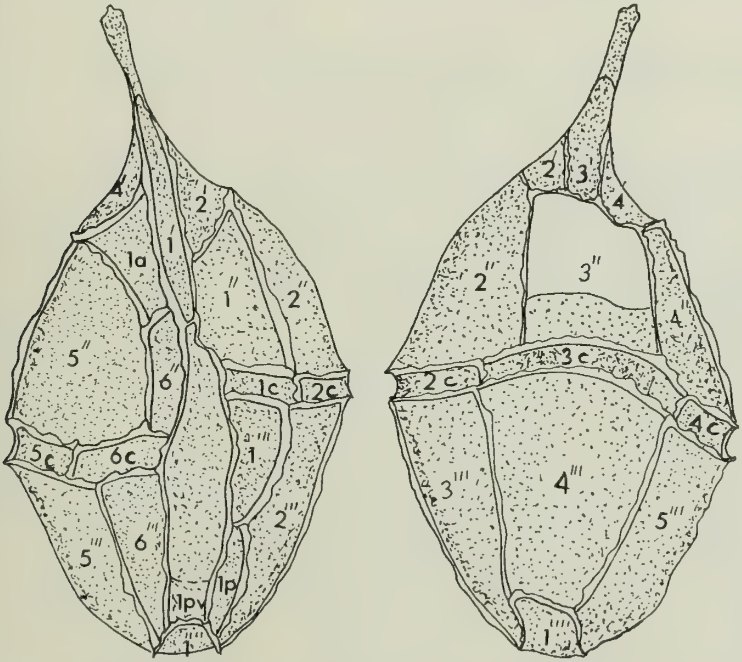


Fig. 14. *Gonyaulacysta* sp. F. Tabulation and archaeopyle formation (the operculum has partially slipped inside the cyst). Left, in ventral view; right, in dorsal view. Specimen BM(NH) slide V.56348 (1). × c.983.

The plate boundaries are marked by crests in the form of very low, thick membranes. The surface of the shell is densely granular. A precingular archaeopyle forms by loss of plate 3″; on the figured specimen, the operculum is partially slipped inside.

FIGURED SPECIMEN: BM(NH) slide V.56348(1). Sample ED 240, from 30 ft above Freshwater Steps Stone Band, Egmont Bight, Dorset. Upper Kimmeridgian (Pectinatus Zone).

DIMENSIONS: Figured specimen: overall length 92μ, breadth 52μ, apical horn length 26μ.

REMARKS: The description of this species was based on a single specimen observed in the assemblages examined. In its overall morphology it is typically a species of *Gonyaulacysta*, but it is markedly different from all previously described species. It may be compared with *G. perforans*, since both have a similarly elongate theca, with long apical horn, and a comparable tabulation, but the crests on the sutures are completely different: *G. perforans* has well developed, porate membraneous crests, whereas this form has low, thick membraneous crests. *G. perforans* apparently has a single-layered wall, but in this species the shell wall is distinctly two layered. This specimen certainly represents a new species of *Gonyaulacysta* but, since the only specimen observed is not well preserved, no new name is given.

Gonyaulacysta sp. G

Plate 6, figures 7–8; text-figure 15

DESCRIPTION: The cyst is broadly ovoidal, with a strong apical horn. Tabulation: 4′, 6″, 6c, 6‴, 1p, ?1pv and 1⁗. The apical plates 1′ and 4′ are broad and long, plates 2′ and 3′ are rounded, smaller. The precingular plates are moderately large, except for plates 1″ and 6″ which are somewhat smaller than the others. Plate 3″ is typically lost in archaeopyle formation. The postcingular plates 1‴, 5‴ and 6‴ are small; in contrast, plates 3‴ and 4‴ are very large and occupy almost the whole dorsal side of the hypotract. The single antapical plate, 1⁗, is quite large and convex; plate 1p is small. On the posterior portion of the sulcus some small plates were suggested, but their presence could not be confirmed: they may constitute a subdivided posterior ventral plate 1pv.

The cingulum is narrow, helicoid, laevorotatory, comprised of six cingular plates. It divides the cyst unequally into two parts, the epitract being smaller than the hypotract. The sulcus is short, mainly confined to the hypotract and broadening posteriorly.

The plate boundaries are marked by high, delicate crests, which have smooth edges and are irregularly perforate. The surface of the shell is densely granular. The dense granulation and high crests render the tabulation difficult to determine.

FIGURED SPECIMEN: BM(NH) slide V.56349(1). Sample HC 243, from c. 100 ft below the Rotunda Nodules, in the base of Hounstout Cliff, Dorset. Upper Kimmeridgian (Pectinatus Zone).

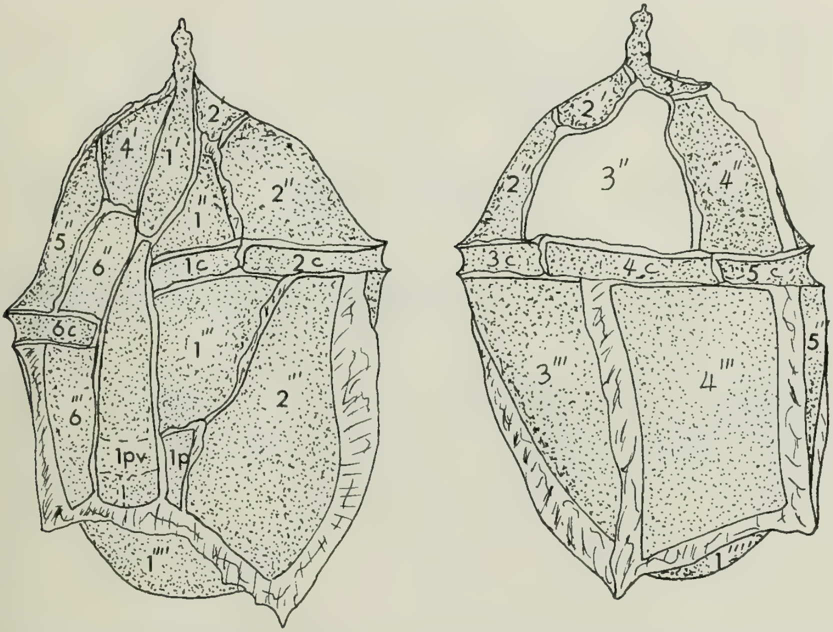


FIG. 15. *Gonyaulacysta* sp. G. Tabulation and archaeopyle formation (plate 3″ is missing). Left, in ventral view; right, in dorsal view. Specimen BM(NH) slide V.56349 (1). × c.1024.

DIMENSIONS: Figured specimen: overall length 75μ, breadth 45μ, apical horn length 10μ, breadth of the cingulum 5μ.

REMARKS: This single specimen differs from the described species of *Gonyaulacysta* in its general shape and distinctive sutural crests. The tabulation and perforate crests are similar to those in *G. perforans*, but in the other morphological characters those species are dissimilar.

Gonyaulacysta sp. H

Plate 13, figure 1, text-figure 16

DESCRIPTION: Cyst subpolygonal to ovoidal, with a strong apical horn of moderate length. The cyst wall is rather thick and composed of two layers, the periphragm alone forming the horn; the surface of the periphragm is densely and finely granular Tabulation 4–?5′, 1a, 6″, 6c, 5‴, op, ?1pv, 1⁗. The sutures are indicated by low ridges, from which arise small prominences, too blunt and short to be called spines. The number of apical plates is doubtful only because a small circular plate appears to cap the horn: four other plates can clearly be seen, plate 1′ being unusually large and broad. Plate 6″ of the precingular series is reduced to accommodate an obliquely positioned anterior intercalary plate: plate 3″ is lost in archaeopyle formation.

The cingulum is narrow and pronouncedly laevorotatory, its two ends differing in antero-posterior position by three times its breadth. The sulcus is broad: it is widely separated from the apex by the enlarged plate 1′, from the antapex (apparently) by a narrow posterior ventral plate, whose boundary was only doubtfully determined.

Only five postcingular plates appear to be present, the first being reduced: no posterior intercalary plate was determinable. The single antapical plate is relatively small.

Figured specimen: BM(NH) slide V.56339(1). Sample CH 231, Kimmeridge Clay (Wheatleyensis Zone) 22 ft below the Blackstone, Clavells Hard, Dorset.

Dimensions: Figured specimen; overall length 120μ, length of apical horn 30μ, breadth 72·5μ, crests c. 1·5μ high.

Remarks: This single specimen certainly represents an undescribed species of *Gonyaulacysta*, characterized by its shape and tabulation. In general proportions, it is akin to a number of other Upper Jurassic and Lower Cretaceous species, all of which, however, have more elaborate crests and a more complex tabulation.

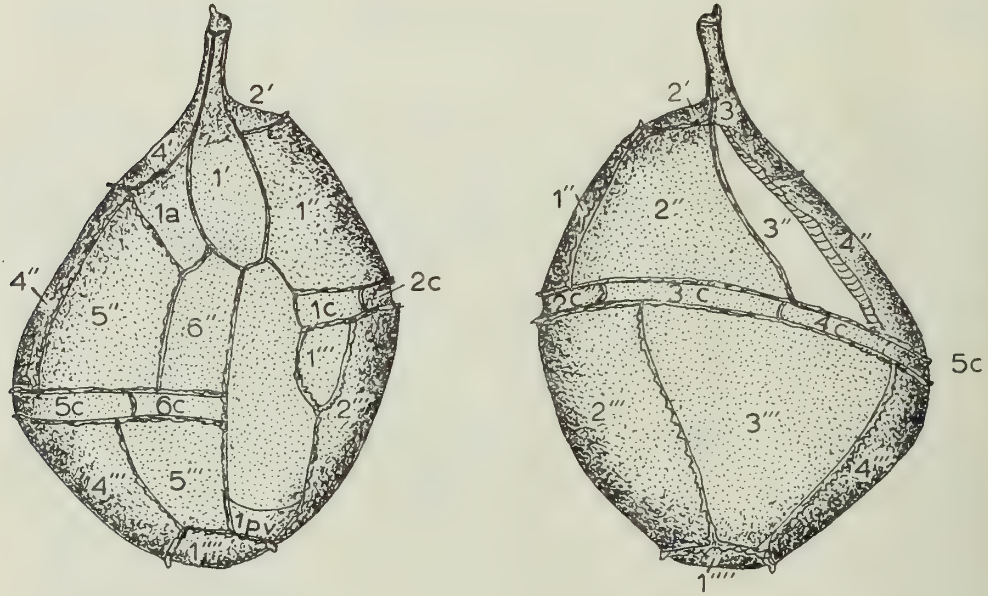


Fig. 16. *Gonyaulacysta* sp. H. Tabulation and archaeopyle formation (plate 3″ is missing). Left, in oblique ventral view; right, in oblique dorsal view. Specimen BM(NH) slide V.56339 (1). × c.640.

Genus ***LEPTODINIUM*** Klement, 1960b emend. Sarjeant, 1969

Leptodinium aceras (Eisenack) Sarjeant, 1969, emend.

Plate 5, figures 1–3, text-figure 17

1958 *Gonyaulax aceras* Eisenack, 391, pl. 2, figs 1–2.
1962 *G. aceras* Eisenack; G. & M. Deflandre, fiche 1752.
1964 *G. aceras* Eisenack; Downie and Sarjeant, 113.
1964 *G. aceras* Eisenack; Eisenack, 311.
1966 *?Gonyaulacysta aceras* (Eisenack); Sarjeant, *nomen nudum*, 131.
1967b *G. aceras* (Eisenack); Sarjeant, *nomen nudum*, table 1.
1967b *Gonyaulax aceras* Eisenack; Vozzhennikova, table II.
1969 *Leptodinium aceras* (Eisenack); Sarjeant, 12.

EMENDED DIAGNOSIS: Cyst broadly ovoidal to subspherical, without appendages, with tabulation 4′, 1a, 6″, 6c, 6‴, 1p, 1pv and 1⁗. Cingulum helicoid, laevorotatory; sulcus narrow, extending on both epitract and hypotract. Sutures in the form of low membraneous crests. Surface coarsely granular. Archaeopyle rarely developed, formed by loss of plate 3″.

HOLOTYPE: Tübingen, Geol.-Paläont. Institut, Pr. 1125, Ob. Apt. Nr. 9. Aptian, North Germany.

FIGURED SPECIMENS: I.G.S. slide PK.108. Sample WB 7, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2834 ft 7 in. depth. Lower Kimmeridgian (Eudoxus Zone).

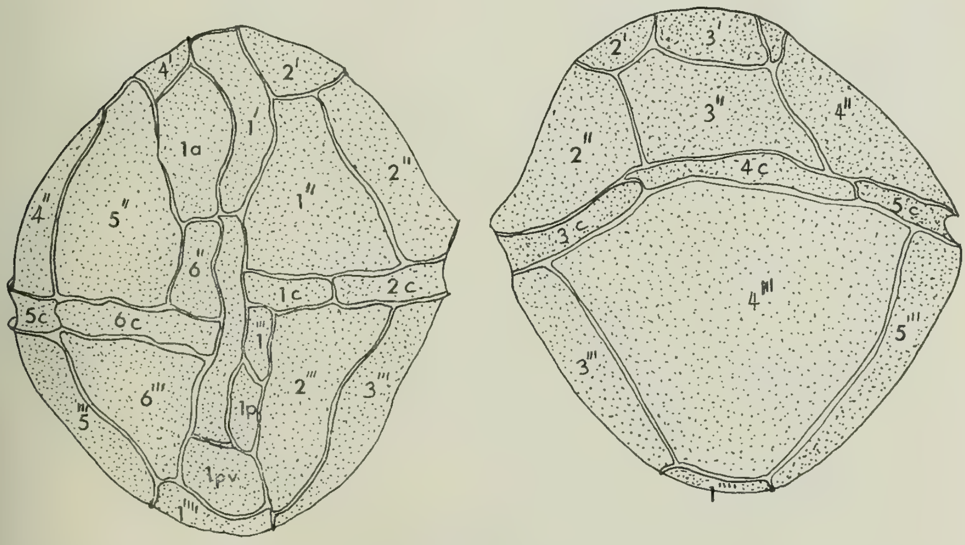


FIG. 17. *Leptodinium aceras* (Eisenack). Tabulation: left, in ventral view; right, in dorsal view. I.G.S. slide PK 108. × c.1041.

I.G.S. slide PK.112. Sample WB 13, from the Warlingham Borehole, at 2684 ft 3 in. depth. Lower Kimmeridgian (Autissiodorensis Zone).

Dimensions: Holotype: overall length 85μ, breadth 71μ. Range of the observed specimens, which are 16 in number; overall length 60–95μ, breadth 52–90μ.

Description: The moderately thick-walled cyst is divided into two unequal parts by the relatively narrow cingulum. The epitract is slightly longer than the hypotract: both are dome-shaped.

Four apical plates, of variable shape and size, make up the apex: plate 1′ is elongate and sigmoidal, almost as long as the sulcus, and extending down two-thirds of the epitract. Plates 2′ and 3′ are quite large; plate 4′ is reduced because of the larger anterior intercalary plate (1a), which is also the reason for the reduction of precingular plate 6″. The other precingular plates are relatively large. The cingular plates are narrow and long, plate 1c being smallest. Six postcingular plates are present, with plate 1‴ reduced and triangular. Plate 4‴ is the largest plate of the cyst. The intercalary plate (1p) is placed below the plate 1‴, its outbulge causing the sulcus to become narrower. A quite large plate, 1pv, separates the single antapical plate 1⁗ from the sulcus and plate 1p.

Observed range: Kimmeridgian (Autissiodorensis to Pectinatus).

Total known range: Kimmeridgian (Autissiodorensis to Pectinatus) and Aptian.

Remarks: The diagnosis is emended to include reference to the tabulation and the mode of archaeopyle formation. (In his original diagnosis, Eisenack was unable to give the tabulation pattern.) Sixteen specimens were observed in the Kimmeridgian assemblages from England: although they were not perfectly preserved, it was possible to determine the tabulation, one of them (the figured specimen) showing it particularly well. A precingular archaeopyle was observed in only two of the specimens; an archaeopyle of this type is figured by Eisenack, who recorded this species from the Aptian of Germany and placed it in *Gonyaulax*. Since it has no apical horn it was transferred to the genus *Leptodinium* by Sarjeant (1969).

Leptodinium amabilis (Deflandre) Sarjeant, 1969

Plate 10, figures 5–6, text-figure 18

1939b *Gonyaulax amabilis* Deflandre, 143, pl. 6, fig. 8.
1941b *G. amabilis* Deflandre; Deflandre, 11, pl. 3, figs 8–9, text-figs 1–2.
1962 *G. amabilis* Deflandre; G. & M. Deflandre, fiche 1755.
1964 *G. amabilis* Deflandre; Downie and Sarjeant, 113.
1964 *G. amabilis* Deflandre; Eisenack, 315–316.
1964 *G. amabilis* Deflandre; Sarjeant, table 2.
1966 *Gonyaulacysta amabilis* (Deflandre); Sarjeant, *nomen nudum*, 130.
1967b *G. amabilis* (Deflandre); Sarjeant, *nomen nudum*, table 1.
1967b *Gonyaulax amabilis* Deflandre; Vozzhennikova, 91, table 11.
1969 *Leptodinium amabilis* (Deflandre); Sarjeant, 12.
1970 *L. amabilis* (Deflandre); Gitmez, 269–70, pl. 12, figs 1–2.

DESCRIPTION: The cyst is broadly ovoidal, with the tabulation 4′, 6″, 6c, 6‴, 1p, 1pv, 1⁗. The strongly spiral cingulum divides the cyst more or less equally. The sulcus is long and extends onto both epitract and hypotract, being narrow on the epitract. Moderately high crests arise from the sutures, distally feebly denticulate or smooth. The surface of the shell is smooth or finely granular. A precingular archaeopyle is sometimes developed, by loss of plate 3″.

FIGURED SPECIMEN: BM(NH) slide V.56350(1). Sample OF 485, from the road side, Montard d'Oignon, France. Lower Kimmeridgian (Mutabilis Zone).

DIMENSIONS: Figured specimen: overall length 38μ, breadth 34μ. Range of the observed specimens (8 in number): length 38–50μ, breadth 34–45μ, sutures length 3–4μ. Deflandre gave the dimensions of the holotype as length 38μ, breadth 32μ. The observed specimens are larger than the holotype.

REMARKS: *L. amabilis* has been previously recorded only from the Kimmeridgian of France. It was infrequent in the samples from England and France, five specimens from the Lower Kimmeridgian (Baylei to Mutabilis Zones) and three specimens from the Upper Kimmeridgian (Pectinatus) being observed. It is recorded from English assemblages for the first time: the mode of archaeopyle formation for this species is also recorded for the first time. In general structure and tabulation, the observed specimens correspond closely to the holotype.

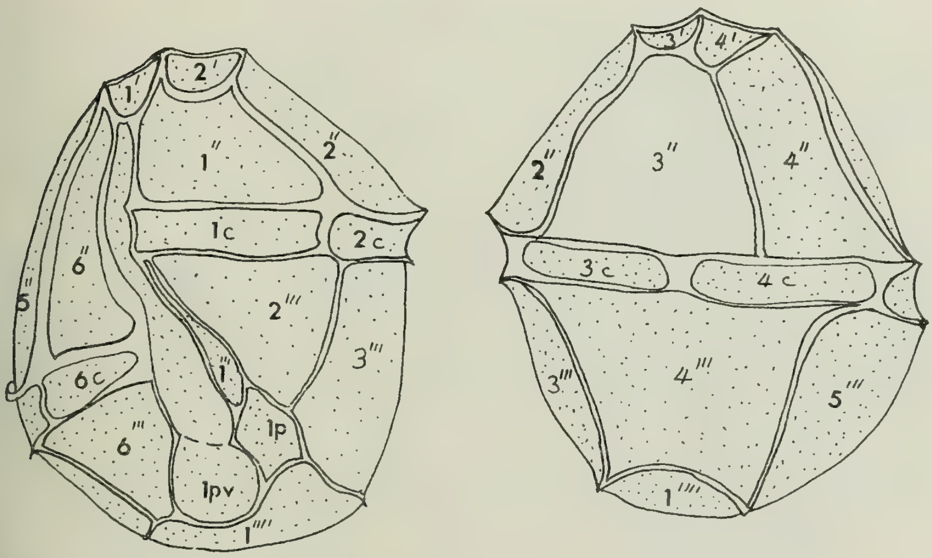


FIG. 18. *Leptodinium amabilis* (Deflandre). Tabulation and archaeopyle formation (plate 3″ is missing): left, in ventral view; right, in dorsal view. Specimen BM(NH) slide V.56350 (1). × c.1690.

***Leptodinium* cf. *crassinervum* (Deflandre) Sarjeant, 1969**

Plate 3, figure 8, plate 5, figures 4–6; text-figure 19

DESCRIPTION: The shell is broadly ovoidal to polygonal in shape. The cyst wall is thick (c. 2·5μ) and densely granular. The crests are membraneous in character and arise from slight thickenings of the periphragm; although they are low, they are quite obvious. They give rise to occasional short spines, up to c. 4–4·5μ in height. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p, 1pv, 1⁗ and 2s. Plate 1′ is elongate, extending down almost two-thirds of the epitract. Plates 2′, 3′ and 4′ are more or less equal in size. The precingular plates are relatively large, except plate 6″ which is reduced because of the large anterior intercalary plate (1a). The six postcingular plates are of variable shape and size: plate 2‴ is reduced to accommodate the intercalary plate (1p) which is rather large. Plate 1‴ is quite small; the other postcingular plates are relatively large, plate 4‴ being the largest of all the plates. A crescent-shaped posterior ventral plate, 1pv, separates the sulcal plates from the single antapical plate.

The cingulum is moderately narrow, formed by six plates (plate 6c is very small); it is slightly spiral, laevorotatory and divides the theca unequally: the epitract is twice as large as the hypotract. The sulcus is short and broad; its posterior portion is formed by two sulcal plates, one small, the second quite large.

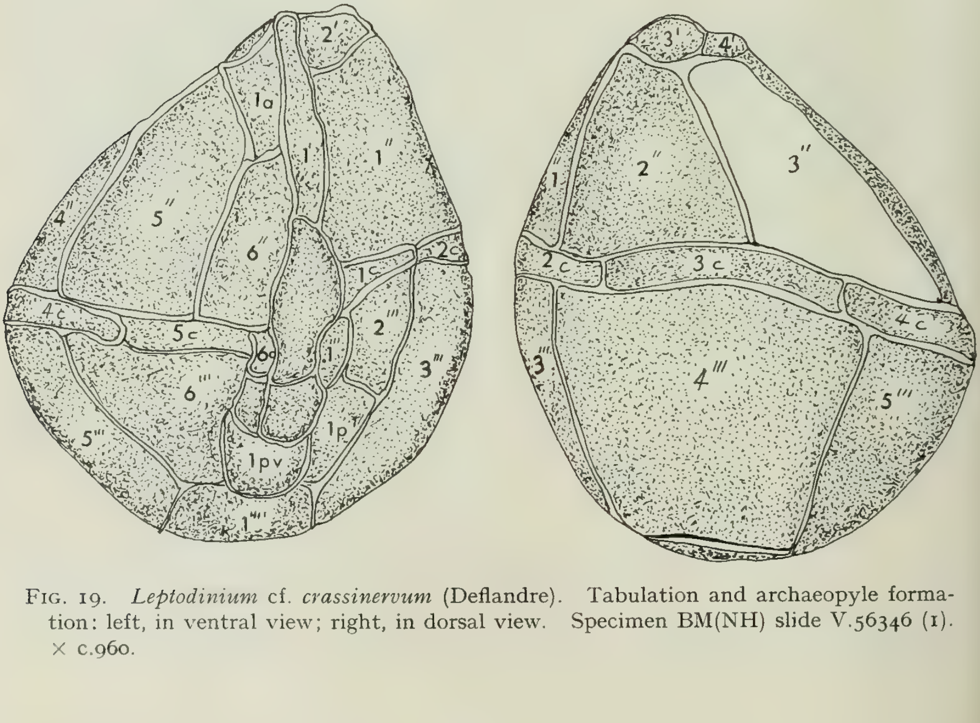


FIG. 19. *Leptodinium* cf. *crassinervum* (Deflandre). Tabulation and archaeopyle formation: left, in ventral view; right, in dorsal view. Specimen BM(NH) slide V.56346 (1). × c.960.

On the dorsal side of the shell, a large precingular archaeopyle is formed by loss of plate 3″.

Figured specimens: BM(NH) slide V.56346(1), (3) and V.56351(1), Sample LO 353 from the Littleworth Quarry, Oxfordshire. Upper Kimmeridgian (Pallasioides Zone).

Dimensions: Range of the observed specimens: overall length 68–80μ, breadth 50–68μ. Measured specimens 4 in number.

Deflandre gave the following dimensions for *L. crassinervum*: length 82μ, breadth 69μ. The English Kimmeridgian specimens found which are similar to Deflandre's specimen, are slightly smaller.

Remarks: *L. crassinervum* has been recorded only from the Kimmeridgian of France (by Deflandre); the species was based on a single specimen and, because of its poor preservation, Deflandre was unable to determine the tabulation. Later Sarjeant re-studied the holotype and, on the basis of its similarity to other Jurassic species, re-attributed it to *Gonyaulacysta*. Recently, it was transferred to *Leptodinium*, on the basis of its lack of an apical horn.

Four specimens observed, all from the Pallasioides Zone of England (sample LO 353), exhibit a strong resemblance, in their long epitract and thick shell wall, to *L. crassinervum*, but could not be attributed to that species with confidence, in absence of knowledge of the tabulation of the holotype.

***Leptodinium* sp.**

Plate 3, figure 9; text-figure 20

Description: Cyst spherical to subspherical, an appearance of polygonality being imparted by the crests. Tabulation: 4′, 1a, 6″, 6c, 6‴, 1p, 1⁗; plate boundaries bearing relatively high, delicate, distally denticulate crests.

The first apical plate, 1′, is long and narrow, occupying the anterior extension of the sulcus. Plates 2′ and 3′ are comparable in shape and size, but plate 4′ is markedly larger. Between the plates 1′ and 4′, a small, elongate intercalary plate (1a) is accommodated. The precingular plates are generally large, except plate 6″, which is narrow. The postcingular plates are also all quite large. Plate 6‴ is slightly reduced. Because of the bad orientation of the specimen, the exact shape and size of plates 1‴ and 2‴ is not very clear, but plates 3‴ and 4‴ appear the largest of all the plates. The single large antapical plate (1⁗) is pronouncedly convex.

The cingulum is strongly helicoid, laevorotatory, occupied by six relatively large cingular plates. It divides the cyst unequally: the sulcus is sigmoidal in shape and extends between the apex and antapex, narrowing to the two ends.

The surface is smooth and the wall is transparent. A precingular archaeopyle formed by loss of plate 3″ was observed in some of the specimens.

Figured specimen: BM(NH) slide V.56352, sample HC 246, from 140 ft below the Massive Bed, Hounstout Cliff, Dorset. Upper Kimmeridgian (Rotunda Zone).

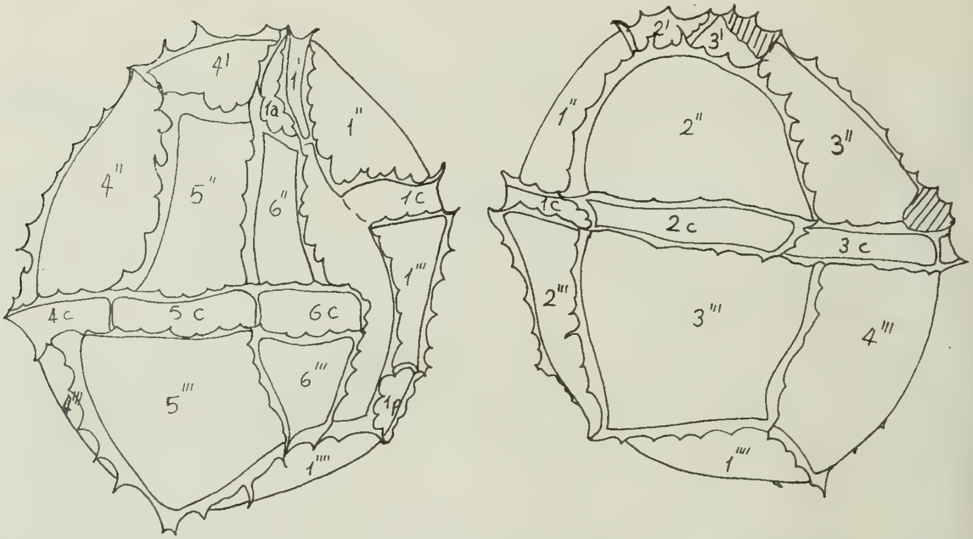


Fig. 20. *Leptodinium* sp. Tabulation and archaeopyle formation (plate 3″ is missing): left, in oblique ventral view; right, in oblique dorsal view. BM(NH) slide V.56352. × c.1620.

Dimensions: Figured specimen: overall length 40μ, breadth 40μ.

Range: Length 40–60μ, breadth 30–52μ. Measured specimens 11 in number.

Observed range: Kimmeridgian (Wheatleyensis to Rotunda).

Remarks: Twelve specimens were observed in the Middle-Upper Kimmeridgian assemblages of England, which are comparable in their morphological features to *Leptodinium*, but differ from the other species of this genus. They possibly represent a new species. Unfortunately, all the specimens observed are somewhat crushed, folded and in a bad orientation; the figured specimen was the best. The small size and the transparent shell wall of the specimens increase the difficulty of determining the tabulation. Accordingly, no new specific name for these forms can yet be proposed.

The most closely comparable species is *L. amabilis*, which is similarly small. However, these Kimmeridgian forms are clearly distinguished by the character of their crests, the presence of an anterior intercalary plate, the absence of the posterior ventral plate and the details of the rest of the tabulation.

Genus ***OCCISUCYSTA*** Gitmez, 1969

Occisucysta evitti (Dodekova) Gitmez, 1970

1969 *Gonyaulacysta evitti* Dodekova, 14–15, pl. 1, figs 1–8, table 1.
1970 *Occisucysta evitti* (Dodekova); Gitmez, 269.

Description: Cyst spherical, with the tabulation 4′, ?1a, 6″, 6–7c, 7‴, 1p, 1pv, 1⁗. No true apical horn appears to be present, the apical prominence being formed by the confluence of crests. The cingulum is strongly helicoid, laevorotatory, dividing the cyst unequally: the epitract is slightly longer than the hypotract. The sulcus is short. The sutures bear delicate, perforate, membraneous crests, with denticulate edges. Around the apex, the crests are apparently higher than elsewhere. The surface is granular and tuberculate, also possessing lines of small spines which form "double sutures", parallel to the true sutures. A precingular archaeopyle is formed by loss of plates 2'' and 3''.

HOLOTYPE: Dodekova's collection, Jmp/DO-16. Tithonian, Bulgaria.

DIMENSIONS: Holotype: overall length 82μ, breadth 82μ, crests 4μ, high on the sutures, apical crests 8μ high.

REMARKS: The description and dimensions mentioned here are as given by Dodekova. This species is characterized by a two-plate precingular archaeopyle. Although Dodekova did not mention the anterior intercalary plate (1a), the photographs of the holotype of *G. evitti* show that the plate above 6'' (which was indicated as plate 4') is, in fact, plate 1a, a boundary being present at its anterior end, separating off a small plate 4'. The position of the plates 7''' and 1pv is exactly the same as in *O. balios*. In tabulation and the character of archaeopyle, therefore, this species corresponds to the genus *Occisucysta* and is accordingly reallocated to it, despite the lack of a true apical horn. Erection of a second genus, to accommodate hornless forms, may prove desirable in the future.

Occisucysta monoheuriskos sp. nov.

Plate 7, figures 10–11, text-figure 21

DERIVATION OF THE NAME: Greek, *monos*, one, single, *heurisko*, find, discover; referring to the discovery of a single specimen.

DIAGNOSIS: A species of *Occisucysta* with a globular cyst. Tabulation: 4', 6'', 7c, 7''', 1p, 1pv, 1'''', 2s. The epitract and hypotract are almost equal in size, separated by the only slightly spiral, laevorotatory cingulum. The sulcus is broad and short, stretching from about mid-point on the epitract to about mid-point on the hypotract. The surface is finely granular and sparsely tuberculate. Sutures are in the form of spine rows; the spines are distally closed, oblate or bifid, generally simple, but the spines near to the apical horn are connected distally and thus appear more complicated. Short spines surround the distal end of the apical horn like a corona. A two-plate precingular archaeopyle is typically present, forming by loss of plates 2'' and 3''.

HOLOTYPE: BM(NH) slide V.56353(1). Sample CS 421, from the Sand Stone dyke, first lower Meleagrinella Band of Eathie Haven, South Cromarty, Scotland, Lower Kimmeridgian (Cymodoce Zone).

DIMENSIONS: Holotype: overall length 70μ, breadth 65μ, horn length 10μ; length of the sutural spines 5μ, length of the spines surrounding the apical horn 3μ.

DESCRIPTION: The cyst wall is relatively thick, c. 1·5μ. The cylindrical horn rises from the top of the dome-shaped epitract and is formed by two of the four apical plates, 1′ and 2′. Plate 1′ is elongate and broad, corresponding in position to the anterior prolongation of the sulcus. The other three apical plates are relatively large and of more or less equal size. The six precingular plates, together with the apical plates, make up the epitract; no intercalary plates are present. Except for plate 6″, which is narrow and elongate, the precingular plates are quite large; plates 2″ and 3″ are lost in archaeopyle formation. The cingulum is occupied by 7 plates of variable size, the first and last (1c and 7c) being small. The ends of the cingulum are widely separated by a very broad sulcus, which widens further in its posterior portion. Two small plates are developed in the mid-portion of the sulcus.

The hypotract is hemi-spherical. The first postcingular plate (1‴) is small, quadrate and placed in the flank of the sulcus. Plate 2‴ is roughly triangular, and, because of the presence of the intercalary plate (1p), is reduced in size. Plates 3‴, 4‴ and 5‴ are very large. Plate 6‴ is narrow and elongate; plate 7‴ is small. The single, convex antapical plate (1⁗) is quite large. Two intercalary plates, 1p and 1pv, together form a crescent shape; 1pv separates the sulcus from the antapex.

REMARKS: *O. monoheuriskos* has been found in only one sample (CS 421) and only one well preserved specimen has so far been observed. Its general shape, tabulation and the sutural features, combined with the two-plate precingular archaeopyle, agree with the diagnosis of the genus *Occisucysta*. Since all the morphologic features are discernible on the one well-preserved specimen, it is proposed without hesitation as a new species of *Occisucysta*.

O. monoheuriskos is distinguished from the two other described species of the genus by its apical horn of different form and aspect, its lack of an anterior inter-

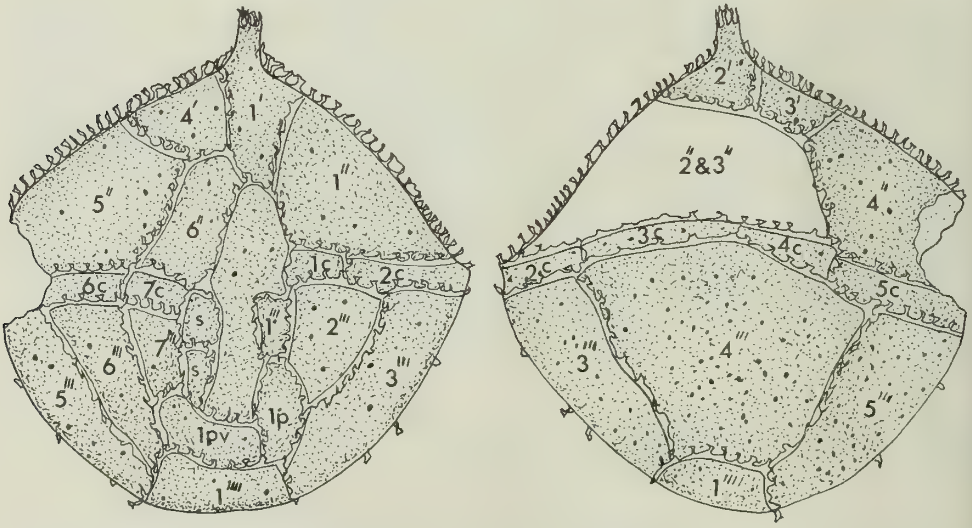


FIG. 21. *Occisucysta monoheuriskos* sp. nov. Tabulation and archaeopyle formation (plates 2″ and 3″ are missing): left, in ventral view; right, in dorsal view. Holotype: BM(NH) slide V.56353 (1). × c.1041.

calary plate, and a number of details of the tabulation. In its possession of a cylindrical apical horn distally surrounded by spines and its spinous sutures, it shows some similarity to *Occisucysta* sp. of Gitmez (1969), but since bad preservation precluded any detailed knowledge of *Occisucysta* sp., an extended comparison is not possible.

Cyst-Family **MICRODINIACEAE** Eisenack, 1964, emend. Sarjeant and Downie, 1966

Genus ***DICTYOPYXIS*** Cookson and Eisenack, 1960b

Dictyopyxis areolata Cookson and Eisenack, 1960b

Plate 7, figure 9

1955 *Membranilarnax ovulum* Valensi, 590, pl. 2, fig. 4, pl. 5, fig. 6.
1960b *Dictyopyxis areolata* Cookson and Eisenack, 255–6, pl. 39, figs 12–14.
1961 *Dictyopyxidia areolata* (Cookson and Eisenack); Eisenack, *nomen nudum*, 316.
1962b *Dictyopyxis areolata* Cookson and Eisenack; Sarjeant, 494, pl. 70, fig. 19; text-fig. 13, tables 2–3.
1964 *Dictyopyxidia areolata* (Cookson and Eisenack); Downie and Sarjeant, *nomen nudum* 110.
1964 *Dictyopyxis areolata* Cookson and Eisenack; Sarjeant, table 3.
1966b *Ellipsoidictyum areolata* (Cookson and Eisenack); G. & M. Deflandre, fiches 3318–9.
1967b *Dictyopyxidia areolata* (Cookson and Eisenack); Sarjeant, *nomen nudum* table 2.
1968 *Dictyopyxis areolata* Cookson and Eisenack; Sarjeant, 229–30, pl. 1, fig. 1; text-fig. 5.
1970 *Dictyopyxis* sp. Gitmez, 275–6, pl. 1, fig. 1, table 4.

DESCRIPTION: This form is characterized by its highly reticulate surface. Each small field is demarcated by high sutures. The cyst is ovoidal to subspherical in shape. The arrangement of reticulae as a pattern of tabulation suggested by Sarjeant (1968) was not determined; however, some small fields on the equatorial plane together form a median line, which may well be equivalent to the cingulum. The apex is lost in archaeopyle formation.

FIGURED SPECIMEN: BM(NH) slide V.53956(1). Sample OM 420, from 20 ft above the Ringstead Coral Bed, west of Osmington Mills, Dorset. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Figured specimen: overall length (apex lacking) 55μ, breadth 50μ. Range of the English specimens (3 specimens were measured): overall length 50–55μ, length without apex 30μ, breadth 40–50μ. Scottish specimens: length (apex lacking) 45–60μ, breadth 40–55μ (3 specimens measured). French specimens: overall length 50–60μ, length without apex 35–50μ, breadth 35–52μ (6 specimens measured).

Cookson and Eisenack gave the range for the Australian specimens as 86–124μ length and 54–66μ breadth, which makes them larger than the European Kimmeridgian specimens.

OBSERVED RANGE: Lower Kimmeridgian (Baylei to Mutabilis).

TOTAL KNOWN RANGE: Upper Callovian (Lamberti) to Lower Kimmeridgian (Mutabilis).

Remarks: *D. areolata* was described originally from the Oxfordian to Lower Kimmeridgian of Australia; subsequently, Sarjeant recorded it from the Oxfordian of England (1962) and the Callovian of France (1968). The specimens illustrated by Valensi as *Membranilarnax ovulum*, from Magdalenian flints of presumed Upper Jurassic age, appear attributable to this species.

Three specimens from Scotland, eight specimens from France and four specimens from England were observed; they occur only in the Lower Kimmeridgian assemblages. These specimens agree in their morphologic features with the holotype of *D. areolata*.

Dictyopyxis cf. ***reticulata*** (Valensi) Sarjeant, 1968

Plate 7, figures 4–5; Plate 12, figures 1–2

Description: The shell is ovoidal with a reticulate surface; the reticulation is irregular. The crests surrounding the small areas are not so high as in *D. areolata*. Spines rise up from the crest nodes; they are solid, simple, oblate or bifid. There is no obvious tabulation, but more regularly formed reticulae make up a median band equivalent to a cingulum. A large apical archaeopyle, with polygonal outline, is developed.

Figured specimens: BM(NH) slide V.56354(1). Sample OF 485, from the road side, Montard d'Oignon, France. Lower Kimmeridgian (Mutabilis Zone).

BM(NH) slide V.56355(1). Sample 486, from the top of the Oignon Beds, west of Lac du Chavoley, France. Lower Kimmeridgian (Mutabilis Zone).

Dimensions: Range of the French specimens (7 specimens measured) overall length 50–61μ, length without apex 30–55μ, breadth 23–65μ, spine length 6–8μ. Scottish specimen: length (apex lacking) 35μ, breadth 48μ. Valensi gave the dimensions for this species as 45μ length (apex lacking) and 52μ breadth, spine length, 3μ. The Kimmeridgian specimens are similar in size, but their spines are longer than those of the holotype.

Remarks: *D. reticulata* was recorded from the Bajocian of Calvados and Bathonian of Vienne, as a species of *Palaeoperidinium*, by Valensi. It was transferred to the genus *Dictyopyxis* by Sarjeant (1968). Single specimens from the Cymodoce Zone of Scotland and France and eight specimens from the Mutabilis Zone of France were recorded, which are closely similar to the specimen figured by Valensi, except for a greater length of the spines arising from the crest nodes. In view of this minor difference in morphology and the stratigraphical hiatus, these nine specimens were compared with, but not placed in, *D. reticulata*.

Genus ***MEIOUROGONYAULAX*** Sarjeant, 1966a

Meiourogonyaulax staffinensis Gitmez, 1970

Plate 9, fig. 4

1970 *Meiourogonyaulax staffinensis* Gitmez, 276–8, pl. 3, fig. 1, text-fig 20 a, b.

Figured specimen: BM(NH) slide V.56356, specimen ED 242, Kimmeridge Clay

(Pectinatus Zone) 60 ft above Freshwater Steps Stone Band, Egmont Bight, Dorset.

Dimensions: Overall length (apex lacking) 84μ, overall breadth 91·5μ, length of cyst alone 72μ, breadth 81·5μ, height of crests 5–9μ.

Range of dimensions: Overall length (apex lacking) 45–98μ, overall breadth 42–91·5μ.

Observed range: Kimmeridgian (Baylei to Pallasioides).

Remarks: This species, hitherto recorded only from the Baylei Zone, ranges throughout the Kimmeridgian (though it has not been encountered in some zones). The size range here quoted is significantly greater than that originally quoted (overall length 48–80μ, overall breadth 45–78μ): the specimen figured is one of the largest encountered.

Meiourogonyaulax dicryptos sp. nov.

Plate 7, figure 6; text-figure 22

Derivation of the name: Greek, *di-*, two, double; *krypto*, cover; referring to the two-layered shell wall.

Diagnosis: Cyst subspherical to spherical, with the tabulation 4′, 6″, 6c, 7‴, 1p, 1⁗, poorly marked by low ridges. Cingulum more or less equatorial and circular. Sulcus deep, short, confined to the hypotract, broadening towards the antapex. Cyst wall thick and composed of two layers: thick endophragm and thin periphragm. The periphragm bulges out on the apex to form a blunt apical horn, a cavity being developed between the two layers. Surface of the cyst is densely granular. Apical archaeopyle always present: sometimes the operculum remains attached to the shell, ventrally.

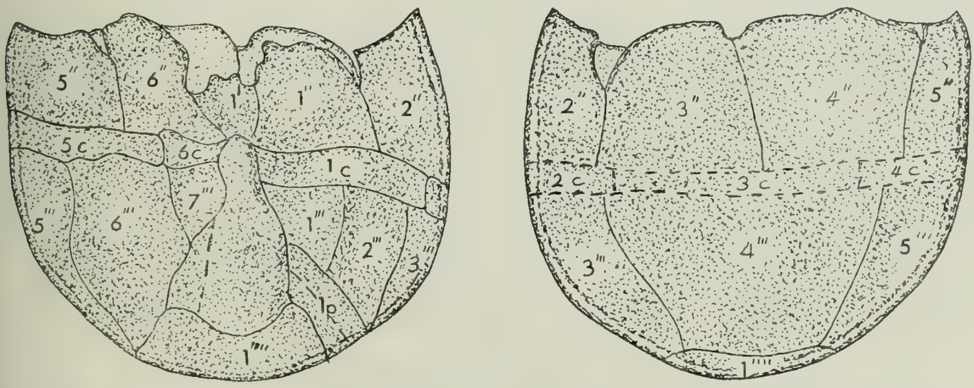


Fig. 22. *Meiourogonyaulax dicryptos* sp. nov. Tabulation and archaeopyle formation: left, in ventral view; right, in dorsal view. Holotype, specimen BM(NH) slide V.56357 (1). × c.1063.

HOLOTYPE: BM(NH) slide V.56357(1). Sample BN 179, from the Marnes à Harpagodes, Benerville, Normandy. Lower Kimmeridgian (Cymodoce Zone).

DIMENSIONS: Holotype: length (apex lacking) 40μ, breadth 52μ.

RANGE: overall length 70–90μ, breadth 52–88μ, length (apex lacking) 40–64μ. Measured specimens 8 in number.

DESCRIPTION: The spherical to subspherical cyst is divided into two equal parts by the moderately narrow cingulum. Both epitract and hypotract are dome-shaped; the epitract bears a small, blunt, hollow apical horn. Four apical and six precingular plates make up the epitract: plate 1′ is elongate, the other apical plates are broader. Plates 1″ and 6″ are somewhat reduced and plates 2″ and 5″ are the largest of the precingular plates. Seven postcingular plates are present on the hypotract. Plates 1‴ and 2‴ are reduced because of the presence of a large intercalary plate (1p). Plates 3‴, 4‴, 5‴ and 6‴ are relatively large; plate 7‴ is reduced. The single antapical plate (1⁗) is quite large and convex. The cingulum is poorly indicated, formed by six plates of variable size. The sulcus is deep and, in its posterior portion, very wide. An apical archaeopyle forms by loss of the apical plates.

OBSERVED RANGE: Kimmeridgian (Cymodoce, Pectinatus and Rotunda Zones).

REMARKS: Eight specimens (one from France, seven from England) were recorded. These specimens differ from the other species of the genus in the character of their tabulation and possession of a hollow apical horn. In the presence of a seventh postcingular plate, this new species differs from the typical *Meiourogonyaulax* tabulation: however, it corresponds in all other respects.

Meiourogonyaulax pila sp. nov.

Plate 4, figure 5, plate 7, figure 3; text-figure 23

DERIVATION OF THE NAME: Latin, *pila*, ball; referring to the shape of the cyst.

DIAGNOSIS: Cyst almost circular in outline, without an apical horn and rounded at the antapex. Wall moderately thin, surface finely granular. Tabulation: 4′, 6″, 6c, 6‴, 1p, 1pv and 1⁗. Plate boundaries faintly indicated. The cingulum forms a feebly laevorotatory spiral. Apical archaeopyle typically present, with operculum attached ventrally.

HOLOTYPE: BM(NH) Slide V.56358; sample FD 236, from ¼ mile west of Freshwater Steps, Dorset. Middle Kimmeridgian (on the boundary of the Pectinatus and Hudlestoni Zones).

PARATYPE: I.G.S. Slide PK.121, sample WB 19, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2535 ft 3in. depth. Middle Kimmeridgian (Wheatleyensis Zone).

DIMENSIONS: Holotype: overall length 60μ, breadth 55μ. Range of the observed specimens (19 in number): length 55–75μ, breadth 55–70μ.

DESCRIPTION: The spherical cyst is divided by the moderately wide and more or less equatorial cingulum into two parts, the epitract and the hypotract; these may

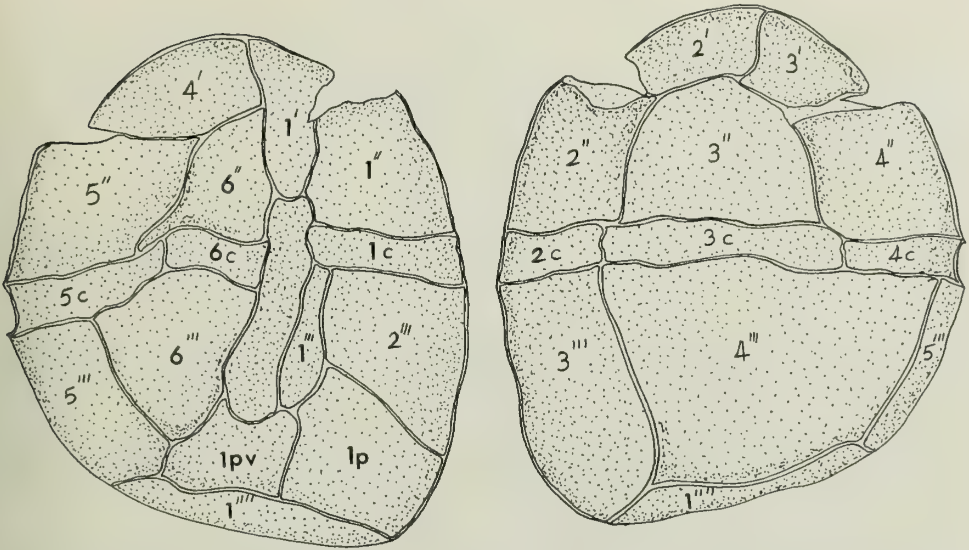


FIG. 23. *Meiourogonyaulax pila* sp. nov. The holotype, with attached operculum. Left, in ventral view; right, in dorsal view. BM(NH) slide V.56358. × c.1018.

be equal in size or the hypotract may be slightly longer than the epitract. The sulcus is relatively short, mainly placed on the hypotract.

Plate 1′ is elongate, the other three apical plates are more or less similar in shape and size. The precingular plates are generally almost equal in size, except that plate 6″ is smaller than the others. The postcingular plates are of variable size: plate 1‴ is relatively small, plate 4‴ is the largest of all the plates. A quite large intercalary plate (1p) is situated between the plates 2‴ and 1⁗; plate 2‴ is correspondingly reduced. A large posterior ventral plate (1pv) separates the sulcus from the antapex. A single antapical plate, broad and slightly convex, occupies the antapex. Plate boundaries are marked by low ridges.

REMARKS: In general appearance, *M. pila* is similar to the members of the genus *Canningia*, for example *C. minor* and *C. ringnesii*; however, since the species of *Canningia* exhibit no tabulation, except for the weakly indicated cingulum, there is no possibility of confusion with *M. pila*. Because of the tabulation and apical archeopyle, the species is clearly attributable to *Meiourogonyaulax*. *M. pila* was recorded from the Middle and Upper Kimmeridgian (Scitulus to Rotunda Zones) from England only: it was not observed in Lower Kimmeridgian assemblages.

Meiourogonyaulax sp.

Plate 4, figure 4, plate 7, figure 12

DESCRIPTION: Cyst broadly ovoidal, almost spherical in shape, without apical horn and with rounded antapex. There is often no indication of tabulation, but in some of the specimens two apical and three precingular plates were recognised with difficulty on the dorsal side. The cingulum is frequently weakly indicated. The cyst wall is thick and is densely granular. An apical archaeopyle is typically present, formed by the rupture of the apex along a more or less straight line with small V-shaped notches along the edge, corresponding to the positions of sutures. Generally, the operculum remains attached ventrally.

FIGURED SPECIMENS: BM(NH) slide V.56359(1). Sample LO 352 from the Littleworth quarry, Oxfordshire. Upper Kimmeridgian (Pallasioides Zone). I.G.S. slide PK.100, sample WB 1, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 7984 ft 7 in. depth. Lower Kimmeridgian (Mutabilis Zone).

DIMENSIONS: Figured specimen from Warlingham Borehole: overall length 75μ, breadth 68μ. Figured specimen from Littleworth: overall length 63μ, breadth 60μ. Range: overall length 48–95μ, breadth 46–85μ. Measured specimens 15 in number.

REMARKS: A group of specimens (22 in number) observed in the Kimmeridgian of England are, in their general appearance, with granular surface and attached operculum, similar to *Canningia ringnesii* (recorded from the Upper Cretaceous of the Arctic by Manum and Cookson, 1964). However, they differ in that they have a relatively thick cyst wall and tabulation (albeit poorly indicated). Because of the mode of archaeopyle formation and the slight indication of a tabulation, these specimens are allocated to the genus *Meiourogonyaulax*. It is possible that they may be intermediate forms between the two genera, in which the tabulation is becoming progressively less apparent.

Genus ***EGMONTODINIUM*** gen. nov.

DERIVATION OF NAME: Named after the type locality—Egmont Bight, Dorset.

DIAGNOSIS: Proximate cyst, spherical to ovoidal. Tabulation typically 4′, 5 or 6 ac., 6″, 6c, 6‴, op, 2pv, 6pc, 1⁗: additional, very small platelets may be developed at crest nodes and the posterior tabulation is subject to some variation. No apical or other horns are developed. Crests or spinelets may arise from the sutures and spines may also be present, singly or in rows, on some plates. Archaeopyle apical, formed by schism along the anterior circle; the operculum frequently remains attached.

TYPE SPECIES: *Egmontodinium polyplacophorum* sp. nov. Kimmeridge Clay (Kimmeridgian: Pectinatus Zone), Egmont Bight, Dorset.

REMARKS: This genus is distinguished from all others yet described in its tabulation. The plates surrounding the apex might be termed anterior intercalaries: the authors, however, feel that this would be inappropriate, since they are not merely interposed between existing reflected plate series but constitute an additional series. The new name "anterior circle plate" is thus coined for them. The plates surrounding the antapex are similarly designated "posterior circle plates", following the precedent of another Jurassic genus, *Pluriarvalium*.

The most comparable genus is *Ellipsoidictyum* Klement 1960, whose complex tabulation was described in detail by Gocht (1970, pp. 150–2): however, the tabulation of the epitract of this genus is markedly dissimilar and a close affinity cannot be considered probable.

The familial allocation of this genus is based on its proximate character and apical archaeopyle: the tabulation does not accord with that specified by its authors for this cyst family and a reallocation may prove necessary in the future.

Egmontodinium polyplacophorum sp. nov.

Plate 8, figures 1–4; Plate 9, figure 3; Plate 11, figures 5–6, 8; text-figure 24

DERIVATION OF NAME: In reference to the large number of plates developed.

DIAGNOSIS: A species of *Egmontodinium* having an ovoidal cyst, thin walled and without prominent granulation or punctation. Sutures variably ornamented with delicate crests or with rows of spinelets, simple or bifurcate and sometimes distally connected; the sutural ornamentation is most prominent around the antapex. The tabulation is as for the genus, but shows some variation in detail through the presence or absence of additional small plates at sutural nodes.

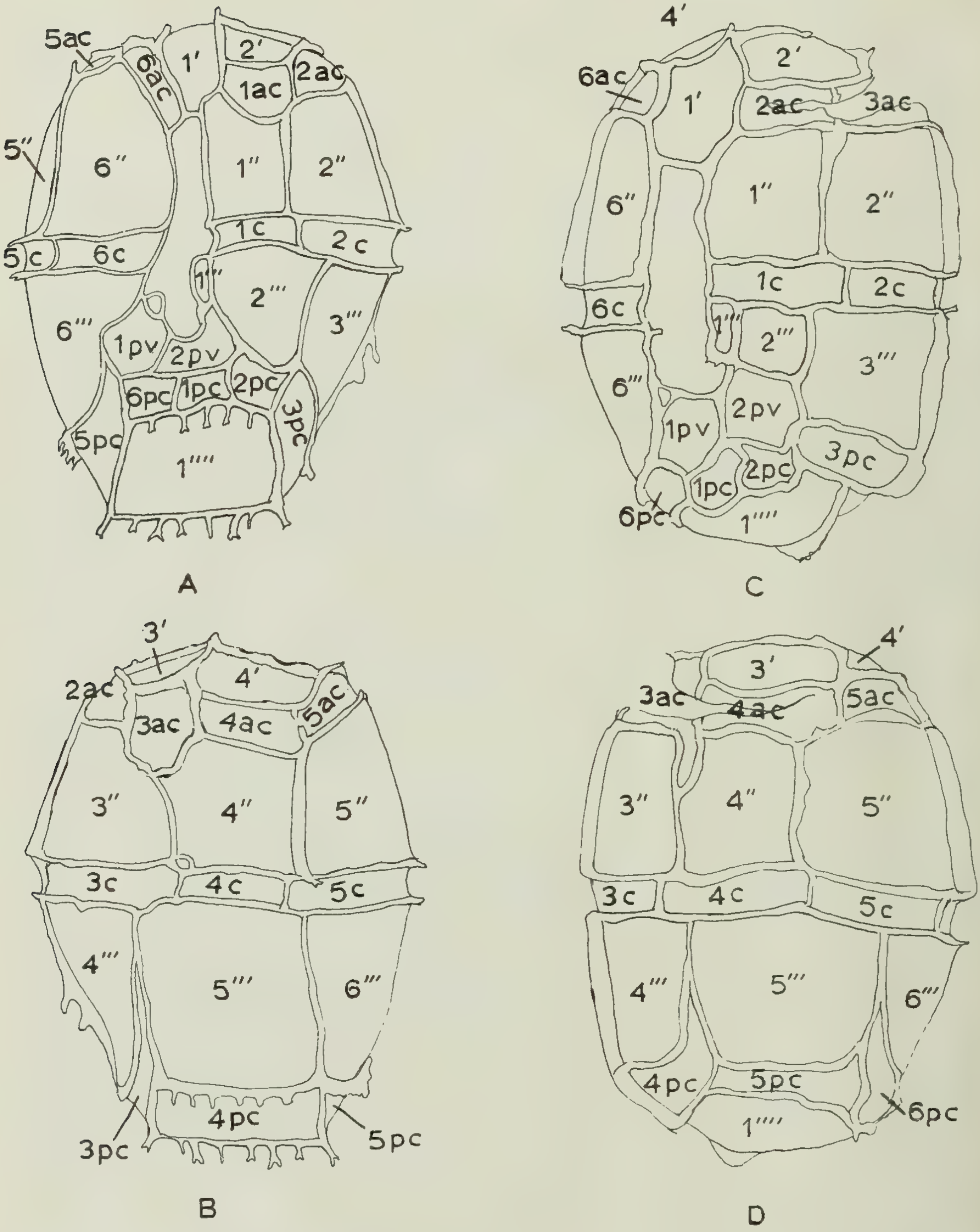
HOLOTYPE: BM(NH) slide V.56360(2b), Kimmeridge Clay (Pectinatus Zone) 60 ft above Freshwater Steps Stone Band, Egmont Bight, Dorset. Paratypes: a. BM(NH) slide V.56360(1). b. BM(NH) slide V.56360(2a), showing apical archaeopyle. c. BM(NH) slide V.56347(1), also showing archaeopyle. [All paratypes are from the same locality and horizon as the holotype.]

DIMENSIONS: Holotype: length of cyst 76μ, breadth 58μ, maximum height of crests 3·5μ. Paratype a: length 78μ, breadth 61·5μ, maximum height of crests 3μ. Paratype b: length (apex lacking) 68μ, breadth 59·5μ, maximum height of crests c. 5μ. Paratype c: length (apex lacking) 61μ, breadth 66μ, maximum height of crests c. 5·5μ. Range: overall length 60–80μ, length without apex 50–68μ, breadth 45–65μ, maximum height of crests c. 3–5μ. Measured specimens: 15.

DESCRIPTION: The cyst surface is typically smooth, but may exhibit minute granulation or punctation. Ornament is normally confined to the sutures: in some instances, however, one or a few isolated spines, or a short row of spines not traversing the plate, may be present within a plate boundary.

Four apical plates are developed, the first being the largest and situated in the anterior prolongation of the sulcus. They are surrounded by six (possibly sometimes by only five) elongate plates constituting the anterior circle, plate 3ac being broader than the others in the holotype. The opercular suture opens along this circle, so that the plate boundaries with the apical plates are present in the operculum and those with the precingular plates on the cyst proper. The initial opening of the opercular suture appears to occur on the dorsal side: the operculum frequently retains a ventral attachment with the abandoned cyst. The holotype shows no opening: paratype (a) is partly open, though the operculum remains attached and almost in place; paratypes (b) and (c) lack the operculum.

The six precingular plates are almost of equal size. In the holotype, a small round plate is present at the node of the crest separating plates 3″ and 4″ and that bounding the operculum: no such plate was distinguished on the paratypes. The


5ac
6ac
1′
2′
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2ac
5″
6″
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1c
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1pv
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4pc
5pc
1⁗
6pc
D

FIG. 24. *Egmontodinium polyplacophorum* gen. et. sp. nov. Reconstruction of the tabulation, A-B Holotype, BM(NH) slide V.56360 (2b) in ventral view and dorsal view. C-D Paratype (a), BM(NH) slide V.56360 (1) in ventral and dorsal view. × c.958.

cingulum is made up of six elongate plates with clear boundaries. The sulcus is broad and occupies only the central part of the ventral surface, being separated from the apex by the large plate 1′ and from the antapex by two posterior ventral plates and by two plates of the posterior circle. In the holotype, a small plate is present at the junction of the sulcus and plate 6‴.

Of the six postcingular plates, the first is extremely small (as is the case in many species of *Gonyaulacysta*) and may be masked by its bounding crests: plate 2‴ is also reduced, to accommodate the second posterior ventral plate, an equivalent of the posterior intercalary plate but displaced to the ventral side. The other four postcingular plates are quite large. The plates of the posterior circle are quite variable in form: in particular, plates 3pc and 5pc sometimes exhibit a remarkable "tail" extending along the sulcus separating two dorsal postcingular plates. The boundaries between the ventral posterior circle plates are in some instances distinguishable only with difficulty, if at all: the holotype is unusually clear in structure and exceptionally favourably orientated. The antapical plate is polygonal and quite large: on two specimens (paratypes a and c) it is partially subdivided by a row of proximally connected spines, but this row only traverses half the plate.

The ornamention of the sutures is highly variable, from rows of isolated, simple or bifurcate spines, with or without distal or (more commonly) proximal connections, to simple delicate crests of moderate height. The highest crests are generally those bounding the cingulum and antapex. (The character of the crests may be modified by accidents of preservation.) The crests or spines are usually little more than one-tenth of the cyst breadth in height: difficulty is often experienced in distinguishing particular crests.

Observed range: Middle to Upper Kimmeridgian (Wheatleyensis to Pectinatus Zones).

Cyst-Family **PAREODINIACEAE** Gocht, emend. Sarjeant & Downie 1966

Genus ***APTEODINIUM*** Eisenack, 1958

Apteodinium cf. ***maculatum*** Eisenack & Cookson

Plate 12, figure 6

Figured specimen: I.G.S. slide PK.105, sample WB 4, from H.M. Geological Survey Borehole, Warlingham, at 2910 ft 6 in. depth. Lower Kimmeridgian (Eudoxus Zone).

Dimensions: Figured specimen: overall length 83μ, breadth 80μ.

Range: (7 specimens measured): length 50–83μ, breadth 45–80μ, apical horn length 3–4μ. Range of the dimensions of Australian specimens, as given by Eisenack and Cookson: length 74–105μ, breadth 70–105μ. The Kimmeridgian specimens are thus of comparable size.

Remarks: Nine specimens recorded, seven from English and two from French assemblages, are similar to *A. maculatum*, as recorded and described from the Albian by Eisenack and Cookson. They differ from the Australian specimens in having a precingular archaeopyle and in the absence of the small thickened areas with circular outlines that give *A. maculatum* its characteristic appearance; in only one specimen, from the Warlingham assemblage, were similar small circular areas observed. The Kimmeridgian specimens must be thus considered only comparable to, and not definitely conspecific with, the Australian specimens.

OBSERVED RANGE: Lower to Middle Kimmeridgian (Baylei to Rotunda Zones). Not yet observed from the Cymodoce and Elegans Zones.

Genus ***IMBATODINIUM*** Vozzhennikova, 1967b

Imbatodinium antennatum sp. nov.

Plate 11, figures 2–3

1970 *Imbatodinium* sp. Gitmez, 282, pl. 7, fig. 5, table 4.

DERIVATION OF THE NAME: Latin, *antenna*, feeler, a sensory appendage on the head of an insect—with reference to the similarity of the process rising up from the apical horn of this species to an insect's antenna.

DIAGNOSIS: A proximate cyst, elongate to ovoidal in shape, with a strong apical horn. On the distal end of the horn, there is a thread-like projection of variable length ending in a small knob. In some cases, a cingulum is weakly developed; but there is no indication of tabulation or sulcus. The surface of the cyst is granular. An intercalary archaeopyle is often developed.

HOLOTYPE: I.G.S. slide PK.124, sample WB 23, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2434 ft 6 in. depth. Middle Kimmeridgian (Hudlestoni Zone).

PARATYPE: BM(NH) slide V.56361(1), sample ED 242, from 60 ft above the Freshwater Steps Stone Band, Egmont Bight, Dorset. Upper Kimmeridgian (Rotunda Zone).

DIMENSIONS: Holotype: overall length 73μ, breadth 35μ, apical horn length without projection 9μ, with projection 16μ. Range of the observed specimens (16 in number): overall length 62–100μ, breadth 28–50μ, overall length of horn 12–30μ, horn length without projection 7–16μ, length of the projection 4–14μ.

DESCRIPTION: The cyst is elongate, broadening in the posterior median region. The apical horn is well developed, bearing a thread-like process of variable length, generally between half and one-third of the overall horn length. This thread-like process ends in a small bulge, which appears as a knob. The cingulum is only weakly developed, but may be suggested by faint surface marking. The epitract is longer than the hypotract, comprising almost two-thirds of the overall length.

OBSERVED RANGE: Lower to Upper Kimmerdigian (Baylei to Rotunda Zones). Not yet observed from the Cymodoce and Elegans Zones.

REMARKS: This new species of *Imbatodinium* is distinguished from the previously described species in its general shape, presence of an intercalary archaeopyle and characteristic shape of the apical horn. In horn shape, it is similar to *I. villosum*, which was recorded from the Upper Jurassic of Russia by Vozzhennikova, but it differs from *I. villosum* in the absence of the sutural spines distributed all over the surface.

I. antennatum is present in the Kimmeridgian assemblages of England, Scotland and France; however, it is infrequent; one specimen from France, one specimen from Scotland and fifteen specimens from England being recorded. It is rare in the Lower Kimmeridgian, in which only four specimens were observed. The number increases in the upper horizons: five specimens were recorded from the Middle Kimmeridgian and seven specimens from the Upper Kimmeridgian.

***Imbatodinium* cf. *villosum* Vozzhennikova, 1967b**

Plate 11, figure 1

Description: The cyst is broadly ovoidal, elongate, with a broad based apical horn, distally bearing a process. There is neither tabulation nor sulcus; the cingulum is only faintly indicated. The epitract is longer than the hypotract, comprising almost three-quarters of the whole length of the cyst. The surface of the cyst is coarsely granular and covered by short, thick spines. An archaeopyle, intercalary in position, is occasionally present.

Figured specimen: BM(NH) slide V.56362(1), sample HC 243, from c. 100 ft below the Rotunda Nodules Bed, Chapmans Pool, Dorset. Upper Kimmeridgian (Pectinatus Zone).

Dimensions: Figured specimen: overall length 80μ, breadth 40μ, horn length 17μ. Range: overall length 70–87μ, breadth 40–52μ, overall length of horn 8–17μ, horn length without process 4–13μ, apical process length 4–6μ; length of the spines over the surface 2·5–4μ. Dimensions of *I. villosum* as given by Vozzhennikova: overall length 70·5–100μ, breadth 27–40·5μ, apical horn length 10·5–13·5μ.

Remarks: Seven specimens observed in the Upper Kimmeridgian (Pectinatus to Pallasioides Zones) assemblages of England are similar to *I. villosum*, but smaller and the spines distributed on the surface are relatively shorter; for these reasons, they are compared with, rather than attributed to *I. villosum*. Vozzhennikova recorded this species from the Upper Jurassic of the Moscow Province, U.S.S.R.

Cyst-family **UNCERTAIN**

Proximate cyst sp. indet.

Plate 11, figures 4, 7, 9

Description: The shell is broadly ovoidal to subspherical, with two blunt apical horns: the apex is rounded. Tabulation is very faintly indicated; four apical plates, six precingular and one antapical plate were determined with difficulty. The cingulum is indicated by inbulges on the sides of the cyst; the sulcus was not observed. The epitract is longer than the hypotract, so far as is determinable from the feeble indications of the cingulum. The archaeopyle is well developed, but in a very different way from the observed archaeopyle types in recorded species: the apex as a whole, together with one of the precingular plates, is thrown off in the archaeopyle formation, though the apex remains attached to the cyst. The surface of the cyst is densely granular; irregularly formed lumps (verrucae) were present on three of the observed specimens.

Figured specimens: BM(NH) slide V.56363(1) and V.56364, sample FD 236, from $\frac{1}{4}$ mile west of Freshwater Steps, Dorset. Middle Kimmeridgian (from the boundary of the Pectinatus and Hudlestoni Zones).

Dimensions: Range of the observed specimens (4 in number): overall length 66–83μ, breadth 60–75μ.

Remarks: Four specimens were observed, in the English Middle and Upper Kimmeridgian assemblages (Wheatleyensis to Rotunda Zones). In its mode of archaeopyle formation, this form is different from all previously described proximate cysts. Because of the bad preservation and dense surface ornamentation, full details of the morphology could not be obtained; in consequence, no new taxon is proposed.

Cyst-Family **ADNATOSPHAERIDIACEAE** Sarjeant and Downie, 1966

Genus ***ADNATOSPHAERIDIUM*** Williams & Downie, 1966

Adnatosphaeridium paucispinum Klement, 1960b, comb. nov.

Plate 10, figures 1–4

1960 *Cannosphaeropsis paucispina* Klement, 72, pl. 10, figs 9–10.
1964 *C. paucispina* Klement; Downie & Sarjeant, 101.
1964 *C. paucispina* Klement; Sarjeant, table 3.

Description: Cyst subspherical to ovoidal in shape, with a thin, smooth shell wall bearing slender, hollow processes, open distally and branched or broad, funnel-shaped, fenestrate. The processes are connected distally by trabeculae. An apical archaeopyle with a zig-zag margin was seen in almost all observed specimens.

Figured specimens: BM(NH) slide V.56365(1) and V.56366(2), sample BN 179, from the Cymodoce Zone of Benerville, Normandy.

Dimensions: Range (8 specimens were measured): length 40–55μ, breadth 35–60μ, length without apex (6 of the measured specimens have apical archaeopyles) 30–50μ, process length 15–30μ.

Observed range: Lower to Middle Kimmeridgian (Cymodoce to Hudlestoni/Pectinatus boundary).

Total known range: Upper Oxfordian (Malm Alph.) to Middle Kimmeridgian (Hudlestoni/Pectinatus Boundary).

Remarks: This species has previously been recorded from the Upper Oxfordian of Germany by Klement (1960). It is now placed in the genus *Adnatosphaeridium* on the basis of the presence of an apical archaeopyle. The observed specimens were recorded from the Lower Kimmeridgian (Cymodoce Zone) of Normandy and Middle Kimmeridgian (Boundary of Hudlestoni and Pectinatus Zones) of Dorset.

Cyst-Family **HYSTRICHOSPHAERIDIACEAE** Evitt, emend. Sarjeant and Downie, 1966

Genus ***CLEISTOSPHAERIDIUM*** Davey, Downie, Sarjeant and Williams, 1969

Cleistosphaeridium sp.

Plate 15, figure 3

Description: The cyst is spherical to subspherical, the wall thin and granular. Transparent processes, approximately 60 in number, are present: they are simple, conical, hollow and closed distally; their length is generally less than one-third of the cyst length. An apical archaeopyle is sometimes developed.

Figured specimen: BM(NH) slide V.56367(1), sample ED 242, from 60 ft above the Freshwater Steps Stone Band, Dorset. Upper Kimmeridgian (Pectinatus Zone).

Dimensions: Figured specimen: Cyst length (apex lacking) 50μ, breadth 50μ, process length 12μ. Range (16 specimens measured): cyst length 38–60μ, length without apex 40–50μ, breadth 38–66μ, length of the processes 10–22μ.

Observed range: Lower to Upper Kimmeridgian (Autissiodorensis to Rotunda Zones). Not yet observed from the Scitulus-Hudlestoni Zones.

Remarks: Although quite a number of specimens (31 in number) were recorded, the preservation was consistently very bad: they were always found covered by debris, so that there was no chance to examine them in detail sufficient to justify giving a specific name. They accord in general appearance, number and type of processes and apical archaeopyle, with the genus *Cleistosphaeridium*. The most similar species is perhaps *C. machaerophorum* Deflandre and Cookson (1955), which was recorded from the Miocene of Australia, but the bad preservation precluded any detailed study.

Genus ***OLIGOSPHAERIDIUM*** Davey and Williams, 1966

Oligosphaeridium pulcherrimum (Deflandre and Cookson) Davey and Williams, 1966

Plate 13, figure 3, text-figure 25

1954 *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson, text-fig. 6, *nomen nudum*.
1955 *H. pulcherrimum* Deflandre & Cookson, 270, pl. 1, fig. 8, text-fig. 21.
1955 *H. pulcherrimum* Deflandre & Cookson; Valensi, 592, pl. 4, fig. 1.
1957 *H. pulcherrimum* Deflandre & Cookson; Delcourt & Sprumont, 59, pl. 1, fig. 4, pl. 2, fig. 12.
1964 *H. pulcherrimum* Deflandre & Cookson; Downie & Sarjeant, 121.
1966 *Oligosphaeridium pulcherrimum* (Deflandre & Cookson); Davey & Williams, 75–6, pl. 10 fig. 9, pl. 11, fig. 5; table 1.
1967b *O. pulcherrimum* (Deflandre & Cookson); Sarjeant, table 6.

1967 *Hystrichosphaeridium pulcherrimum* Deflandre & Cookson; Clarke and Verdier, 54–5 pl. 10, figs 4–5.
1970 *Oligosphaeridium pulcherrimum* (Deflandre & Cookson); Gitmez, 290 pl. 7, fig. 7, table 4.

DESCRIPTION: The subspherical cyst possesses processes of two types. Some processes are tubular, distally open, widening distally and assuming a funnel shape with fenestrate walls (characteristic for this species); the other processes are simple, bifid or foliate. Because of the complication of the processes and bad preservation, accurate determination of the reflected tabulation was not possible, but the tabulation 6″, 5‴, 1p, 2⁗, 3s may be suggested, with five additional simple processes that could not be named and appear random in distribution. The surface of the shell is smooth. Apical archaeopyle developed.

FIGURED SPECIMEN: BM(NH) slide V.56368(1), sample CC 449, from c. 10 ft from the top of the Calcaires du Moulin Wibert, Cap de la Crèche, Boulonnais. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Figured specimen: length (apex lacking) 40μ, breadth 50μ, process length 25–28μ. Range (4 specimens observed): length (apex lacking) 35–48μ, breadth 45–55μ, process length 18–35μ. Dimensions of the holotype: overall diameter c. 118μ, process length 26–38μ (as quoted by Deflandre and Cookson).

REMARKS: This species first recorded from the Jurassic by Gitmez (1970). Unfortunately, all specimens observed are in too poor condition for examination in detail. Four specimens were recorded, all from the Lower Kimmeridgian (Baylei Zone) assemblages, two of them from Dorset and two from France.

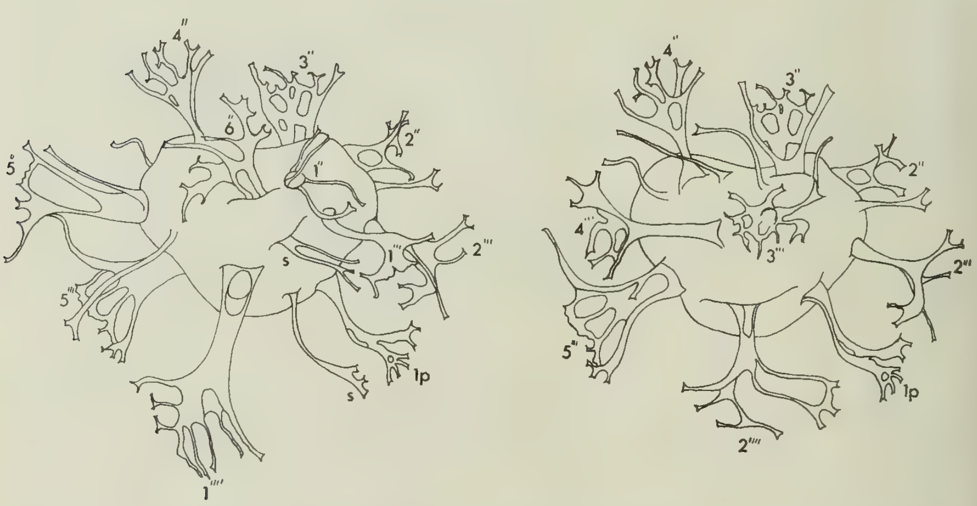


FIG. 25. *Oligosphaeridium pulcherrimum* (Deflandre & Cookson). Specimen showing the suggested tabulation: left, in ventral view; right, in dorsal view. BM(NH) slide V.56368 (1). × c.643.

Genus ***SYSTEMATOPHORA*** Klement, 1960b

Systematophora ovata sp. nov.

Plate 14, figures 1–3

1970 *Systematophora* sp. Gitmez, 296, pl. 8, fig. 5, table 4.

Derivation of the name: Latin, *ovatus*, egg-shaped, with reference to the shape of the cyst.

Diagnosis: A species of *Systematophora* having an elongate, ovoidal cyst bearing short processes (not more than one-fourth of the cyst breadth). The processes are located in groups: there are ten such groups, one occupying the apex, an opposite one the antapex, whilst eight groups are distributed between the apex and the antapex, four of them on the epitract, the other four on the hypotract. There is no connection between the groups of processes or between the processes in each group. The processes are simple, bifid distally or broad based, foliate and deeply forked at their distal end. The surface of the shell is finely granular. When an archaeopyle is developed, it is apical in position.

Holotype: BM(NH) slide V.53962(1), sample SC 444, from the Great Ouse River Board Pit, Stretham, Cambridgeshire. Lower Kimmeridgian (Baylei Zone).

Paratype: BM(NH) slide V.56343(2), sample HC 243, from c. 100 ft below the Rotunda Nodules, Hounstout Cliff, Dorset. Upper Kimmeridgian (Pectinatus Zone).

Dimensions: Holotype: shell length (apex lacking) 35μ, breadth 28μ, process length 6–8μ. Paratype: shell length 58μ, breadth 40μ, process length 8μ. Range: shell length 58–60μ, apex lacking 35–48μ, breadth 28–45μ, process length 8–11μ. Measured specimens were 6 in number.

Description: The cyst wall is composed of two layers, the periphragm forming the processes. Both of the layers are thin and transparent. There is no connection between the processes at their proximal and distal ends; they arise separately from each other, positioned around the margins of ovoidal or polygonal fields whose shape is clearly shown by the broad bases of the processes.

Remarks: This new species was observed very infrequently in the Lower and Upper Kimmeridgian: one specimen was recorded from the Baylei Zone, three specimens from the Pectinatus Zone and one specimen from the Pallasioides Zone of England. Only one specimen was observed in the Scottish assemblages and none from France. The preservation of the specimens was moderately good. This new species differs from all previously described species of the genus on the basis of shape and character of its processes, in combination with the shape of the cyst.

Cyst-Family **UNCERTAIN**

Genus ***STEPHANELYTRON*** Sarjeant, 1961a

Stephanelytron redcliffense Sarjeant, 1961a

Plate 14, figure 6

1960c Organism A. Sarjeant, 404, pl. 13, fig. 13, table 2.
1961a *Stephanelytron redcliffense* Sarjeant, 109–110, pl. 15, fig. 11, text-figs 10, 15.
1962a *S. redcliffense* Sarjeant; Sarjeant, table 4.
1962b *S. redcliffense* Sarjeant; Sarjeant, 495, pl. 70, fig. 7, tables 2–3.
1964 *S. redcliffense* Sarjeant; Downie and Sarjeant, 146.
1964 *S. redcliffense* Sarjeant; Sarjeant, table 4.
1967 *S. redcliffense* Sarjeant; Brito, pl. 2, fig. 3.
1968b *S. redcliffense* Sarjeant; Sarjeant, 225, pl. 3, fig. 5, table 2A.

DESCRIPTION: The cyst is broadly ovoidal, rounded at both ends. The tubular processes extend down the flanks in six rows and surround the apex and antapex in transverse rows; there is also a median transverse row of processes. A corona, broad-based and bearing striations, is present on the antapex. The cyst wall is composed of two layers; both are thin and transparent, without ornamentation. The periphragm forms the processes. There is no connection between the central cavity and the cavity of processes. An apical archaeopyle is typically developed.

FIGURED SPECIMEN: BM(NH) slide V.56366(1), sample BN 179, from the Cymodoce Zone of Benerville, Normandy.

DIMENSIONS: Figured specimen: cyst length 40μ, breadth 32μ, process length 5μ, corona length 8μ. Range: length 40–60μ, length (apex lacking) 45–50μ, breadth 32–45μ, process length 4–5μ, corona length 5–8μ. Measured specimens 4 in number. Holotype dimensions, as given by Sarjeant: length 36μ, breadth 30μ, process length 5μ, corona length 10μ. The Kimmeridgian specimens exhibit similar dimensions, except in the length of the corona, which is greater in the holotype.

REMARKS: This species was originally recorded from the Oxford Clay of England, and later from the Lower Oxfordian of Normandy, by Sarjeant (1961, 1968). Five specimens, all from the same horizon in the Cymodoce Zone of Normandy, were observed, which are closely similar to those figured by Sarjeant.

***Stephanelytron* cf. *redcliffense* Sarjeant, 1961a**

Plate 14, figure 7

DESCRIPTION: Two specimens, also from the Cymodoce Zone, show a general resemblance to *S. redcliffense* but differ in that the processes are markedly thinner. Forms of intermediate character were not encountered.

FIGURED SPECIMEN: BM(NH) Slide V.56365(2), sample BN 179 from the Cymodoce Zone of Benerville, Normandy.

DIMENSIONS: Figured specimen: cyst length (apex lacking) 35μ, breadth 30μ, process length 5μ, corona length 7μ. The second specimen could not be measured because of its bad preservation and orientation.

REMARKS: These two specimens from the Lower Kimmeridgian (Cymodoce Zone of France) may represent a new species or might be extremes in the range of morphological variation of *S. redcliffense*. Fuller information must be awaited.

Cyst-Family **ENDOSCRINIACEAE** Vozzhennikova, emend. Sarjeant and Downie, 1966

Genus ***ENDOSCRINIUM*** Klement, 1960b emend. Vozzhennikova, 1967a

Endoscrinium sp.

Plate 14, figures 9–11, text-figure 26

Description: A species of *Endoscrinium* possessing a subspherical to broadly ovoidal periblast, without apical or antapical horns. The periphragm is irregularly studded with pores of varying shapes and sizes; the endophragm is finely granular. The sutural crests are well defined, in the form of low ridges. Reflected tabulation: 4′, 6″, 6c, 5‴, 1p, 1pv, 1⁗ and 8s. Plate 1′ is elongate, plates 2′ and 3′ are relatively small, the boundary between them was not confirmed; plate 4′ is quite large. The precingular plates and postcingular plates are large, plate 3‴ being the largest of all the plates. The cingulum is strongly laevorotatory, occupied by six plates; plates 1c and 6c are greatly reduced, the other cingular plates are of constant size. The cingulum divides the cyst more or less equally. The sulcus is broad, occupied by sulcal plates of varying shape and size.

A precingular archaeopyle is developed, and formed by loss of plate 3″.

Figured specimen: BM(NH) slide V.56369(1), sample OF 485, from well-bedded calcilutite, Montard d'Oignon, France. Lower Kimmeridgian (Mutabilis Zone).

Dimensions: Figured specimen: overall length 78μ, breadth 75μ, endoblast length 60μ, breadth 55μ.

Remarks: Only one well preserved specimen has so far been observed. The

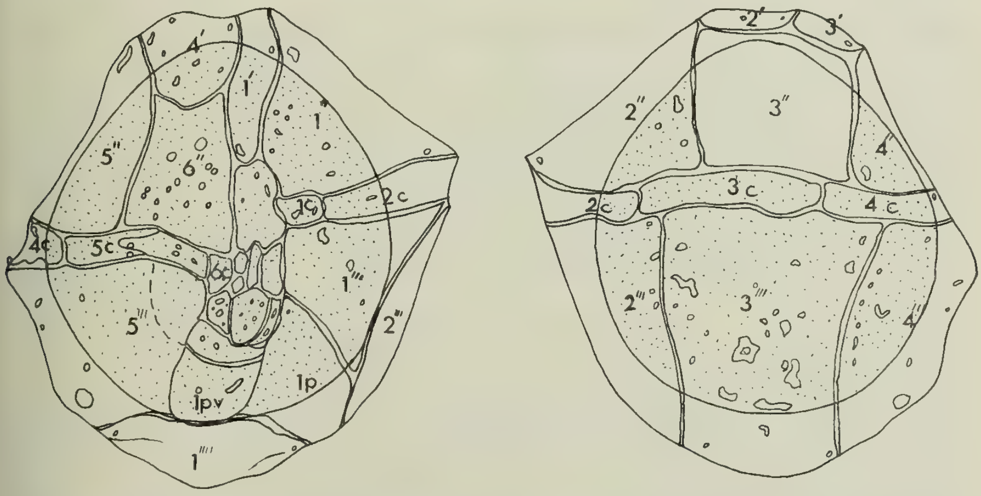


Fig. 26. *Endoscrinium* sp. Tabulation and the archaeopyle formation: left, in ventral view; right, in dorsal view. Specimen BM(NH) slide V.56369 (1). × c.836.

perforation of the periblast and the presence of sulcal plates distinguish this species from all described forms. The general appearance of the cyst and the tabulation are most comparable to *E. luridum*, suggesting a relationship between two species.

Cyst-Family **HEXAGONIFERACEAE** Sarjeant & Downie, 1966

Genus ***HEXAGONIFERA*** Cookson and Eisenack, 1961a emend. Cookson and Eisenack, 1962

Hexagonifera jurassica sp. nov.

Plate 14, figures 5, 8

1970 *Hexagonifera* sp. Gitmez, 2, pl. 1, fig. 12, table 4.

DERIVATION OF THE NAME: So named because this is the first species of the genus observed in Jurassic assemblages.

DIAGNOSIS: A species of *Hexagonifera* with broadly ovoidal to elongate cyst. The periblast has a blunt, hollow apical projection formed by the periphragm only. The surface of the periblast is delicate, smooth or minutely granular: the endoblast, in contrast, is thick-walled and densely granular, with occasional tubercles. A circular cingulum divides the periblast almost equally; sometimes the epitract is slightly smaller than the hypotract. There is no definite indication of tabulation or of a sulcus. An apical archaeopyle is typically developed.

HOLOTYPE: I.G.S. slide PK.123, sample WB 20, from H.M. Geological Survey Borehole, Warlingham, at 2510 ft depth. Middle Kimmeridgian (Wheatleyensis Zone).

PARATYPE: BM(NH) slide V.53621(1), sample SS 627, from 100 ft above the second dolerite sill, Staffin Bay, Skye. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Holotype: overall length 85μ, breadth 72μ, endoblast length 73μ, breadth 66μ, Paratype: overall length (apex lacking) 46μ, breadth 50μ, endoblast length (apex lacking) 40μ, breadth 42μ. The size range of specimens from different horizons is shown in Table 1; according to these measurements, the Lower Kimmeridgian specimens are smaller than those from the Middle and Upper Kimmeridgian. (There is only a slight size difference between the Middle and Upper Kimmeridgian specimens). No dimensional difference was observable between the English and French specimens.

OBSERVED RANGE: Lower to Upper Kimmeridgian (Baylei to Pallasioides). Not yet observed from the Cymodoce, Mutabilis, Elegans and Scitulus Zones.

DESCRIPTION: The subspherical to ovoidal endoblast is completely enclosed by the delicate periblast. The epitract of the periblast is conical, with no apical projection superimposed on the cone shape. The epitract of the endoblast is rounded and dome-shaped. The antapex of both periblast and endoblast is rounded. A polygonal apical archaeopyle is usually present; generally the operculum remains attached to the shell. The tabulation is generally indeterminable, but the dorsal tabulation could be distinguished with difficulty on some specimens: two apical, three precingular, three postcingular and one antapical plates were recognised.

REMARKS: This new species is distinguished from previously described species of the genus by the presence of a cingulum and poorly developed tabulation.

These specimens are similar to *H. chlamydata* Cookson & Eisenack, (1952) in having a granular endoblast, but it is impossible to compare the periblast since it is usually badly preserved or not preserved at all. The presence of a slight apical prominence, a cingulum and poorly developed tabulation distinguish this species from *H. chlamydata*.

TABLE 2

Range of the dimensions of **Hexagonifera jurassica** from the different levels of the Kimmeridgian

	Lower Kimmeridgian	Middle Kimmeridgian	Upper Kimmeridgian
Periblast:			
Length	45–50μ	70–102μ	80–105μ
Length without apex	42–55μ	60–75μ	55–70μ
Breadth	35–56μ	58–90μ	50–90μ
Endoblast:			
Length	40–48μ	58–88μ	65–90μ
Length without apex	38–59μ	55–75μ	45–65μ
Breadth	35–52μ	58–75μ	45–75μ
Measured specimens	12	29	19

Cyst-Family **MUDERONGIACEAE** Neale & Sarjeant, emend. Sarjeant & Downie, 1966

Genus ***MUDERONGIA*** Cookson & Eisenack, 1958

Muderongia simplex Alberti, 1961

Plate 15, figures 1–2

1961 *Muderongia simplex* Alberti, 12, pl. 2, figs 1–6, pl. 12, figs 1–2, table c.
1964 *M. simplex* Alberti; Downie & Sarjeant, 134.
1964 *M. simplex* Alberti; Eisenack, 525–6.
1966b *M. simplex* Alberti; G. & M. Deflandre, fiches 3249–50.
1967b *M. simplex* Alberti; Sarjeant, table 12.

DESCRIPTION: The cyst is flattened, bearing an apical, two lateral and two antapical horns. Its outline is almost rhombic, as a result of differential development of the horns. The lateral horns are short and rounded at their free end. The antapical horns are unequal in length; one of them is very short and blunt, the other is well developed. The endoblast lies close to the outer margin of the periblast, generally stretching out into the horns but not reaching their tips, so that lateral, apical and antapical pericoels are present. The tabulation is not well indicated but lines on the epitract, observable only with difficulty, simulate plate boundaries. A narrow cingulum is present but poorly marked. Both periphragm and endophragm are transparent; the surface of the periblast is granular. A well-developed apical archaeopyle was observed in one of the specimens; the other specimens observed often have a split on the flank of the apical region, indicating that the archaeopyle has not developed fully.

Figured specimens: I.G.S. slides PK.128 and PK.129, sample WB 29, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2285 ft 7 in. depth. Upper Kimmeridgian (Rotunda Zone).

Dimensions: Range of the observed specimens (11 in number): overall length 78–110μ, breadth 68–90μ, endoblast length 65–88μ, breadth 55–75μ, overall length (without apex) 70μ, endoblast length (without apex) 48μ. Alberti gave the following ranges from Cretaceous specimens of the species: overall length 68–175μ, breadth 63–133μ.

Remarks: *M. simplex* has been recorded from Valanginian to Barremian of Poland, Bulgaria and Germany. Eleven specimens were recorded, for the first time from England and the Jurassic, all from one horizon, the Rotunda Zone of the Warlingham Borehole. These specimens are similar to the specimens figured by Alberti, the only difference being that the apical horn is not so long as the apical horn of previously recorded specimens and the notches at the ends of the lateral horns were not seen on the Kimmeridgian specimens. With its second, blunt antapical horn, *M. simplex* is similiar to the type species of the genus, *M. mcwhaei*, but it differs in its short and rounded-ended lateral horns, whereas those of the type species are long and curved, downwardly directed.

Cyst-Family **NELSONIELLACEAE** Eisenack, emend. Sarjeant & Downie, 1966

Genus ***SCRINIODINIUM*** Klement, 1957

Scriniodinium bicuneatum (Deflandre) Sarjeant, 1967a

Plate 15, figure 4

1938 *Palaeoperidinium bicuneatum* Deflandre, 180, pl. 8, fig. 7.
1957 *P. bicuneatum* Deflandre; Downie, 422, pl. 20, fig. 2, table 1.
1964 *P. bicuneatum* Deflandre; Downie & Sarjeant, 137.
1964 *P. bicuneatum* Deflandre; Eisenack, 591–2.
1964 *P. bicuneatum* Deflandre; Sarjeant, table 2.
1967a *Scriniodinium bicuneatum* (Deflandre); Sarjeant, 248.
1967b *S. bicuneatum* (Deflandre); Sarjeant, table 11.
1970 *S. bicuneatum* (Deflandre); Gitmez, 308, pl. 5, fig. 5, table 4.

Observed range: Lower to Upper Kimmeridgian (Baylei to Pallasioides). Not yet recorded from the Elegans and Scitulus Zones.

Total known range: Oxfordian (prob. Cordatum)—Kimmeridgian (Rotunda).

Figured specimens: BM(NH) slide V.56370, sample MR 547, from the lower boundary of the Platynota Zone (Baylei Zone), west side of the Ravin d'Enfer, Crussol, France.

DIMENSIONS: Range: overall length 80–115μ, breadth 65–100μ, endoblast length 75–90μ, breadth 62–83μ. (Measured specimens 36 in number). Holotype dimensions, as given by Deflendre, are 100μ length, 65μ breadth, well within the quoted range.

REMARKS: *S. bicuneatum* was originally recorded from the Oxfordian of Normandy; the species was based on a single specimen which was not well preserved. In 1957, it was, for the first time, observed in the English assemblages, when Downie recorded it from the Pectinatus Zone of Dorset. His specimens also were poorly preserved.

It is abundantly present in the Kimmeridgian samples examined from England (55 specimens being recorded); but rare in Scottish and French assemblages (5 specimens from the Baylei Zone of France and only one from the Cymodoce Zone of Scotland). The preservation was generally not good. The presence or absence of an endoblast was not confirmed by Deflandre, nor later by Sarjeant, who re-examined the holotype, noted the general similarity to the members of *Scriniodinium* and redesignated this species as *S. bicuneatum*: its presence can now be confirmed.

The authors consider that Deflandre's figures are in an inverse orientation, with antapex uppermost. The figured specimen is shown in the correct orientation: the ventral tabulation is not discernible, but apical, pre- and postcingular plate series can be distinguished without difficulty.

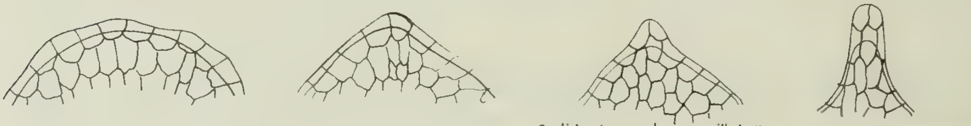
Scriniodinium dictyotum Cookson & Eisenack, 1960a

Plate 15, figures 5–7, Plate 16, figure 6; text-figure 27

1960a *Scriniodinium dictyotum* Cookson & Eisenack; 248–9, pl. 37, figures 8, 9.
1962a *S. dictyotum* Cookson & Eisenack: Sarjeant, 262, pl. 1, fig. 9, tabs 3–4.
1962b *S. dictyotum* Cookson & Eisenack: Sarjeant, pl. 69, fig. 11.
1964 *S. dictyotum* Cookson & Eisenack: Downie & Sarjeant, 145.
1964 *S. dictyotum* Cookson & Eisenack: Eisenack, 755.
1964a *S. dictyotum* Cookson & Eisenack: Sarjeant, table 2.
1967 *S. dictyotum* Cookson & Eisenack: Sarjeant, table 11.
1968 *S. dictyotum* Cookson & Eisenack: Sarjeant, 236, pl. 1, fig. 7, table 2b.
1970 *S. dictyotum* Cookson & Eisenack: Gitmez, 310.
1970 *S. dictyotum* subsp. *dictyotum* Cookson & Eisenack: Gitmez, 310.
1970 *S. dictyotum* subsp. *osmingtonensis* Gitmez, 310–11, pl. 1, fig. 3, pl. 8, fig. 12.
1970 *S. dictyotum* subsp. *papillatum* Gitmez, 311, pl. 9, fig. 11.
1970 *S. dictyotum* subsp. *pyrum* Gitmez, 311–13, pl. 13, figs 1–2, pl. 10, figs 1: Text-fig. 33a–b.

REMARKS: A text-figure clarifying the differences (in form of the apex) between the four subspecies distinguished by Gitmez (1970) is here presented. The typical subspecies, *S. dictyotum dictyotum*, was not encountered in the basal Kimmeridgian, although recorded by Sarjeant (1962a, 1962b, 1964a, 1967b) from the Oxfordian of England and France: four specimens were, however, obtained from the Pectinatus Zone (specimen ED 240) of Dorset. The other subspecies were found only in the Lower Kimmeridgian: observed ranges:

S. dictyotum osmingtonensis Baylei only: Dorset.
S. dictyotum papillatum Baylei to Mutabilis: Dorset and France.
S. dictyotum pyrum Baylei only: Dorset and France.



S. dictyotum subsp. osmingtonensis S. dictyotum subsp. dictyotum S. dictyotum subsp. papillatum S. dictyotum subsp. pyrum

FIG. 27. *Scriniodinium dictyotum* (Cookson & Eisenack). Diagram showing the variation in the character of the apex in the four subspecies of the above.

Scriniodinium sp.

Plate 13, figure 4

DESCRIPTION: The periblast is broadly ovoidal, with a hollow apical horn and rounded antapex. The surface of the periblast is smooth. The endoblast is subspherical to elongate, with rounded ends; its surface is smooth or minutely granular. Boundaries of reflected plates were indicated very feebly or not at all; in consequence, the tabulation could not be determined. The cingulum is relatively narrow and slightly helicoid, laevorotatory. A broad sulcus could be distinguished on some of the specimens observed. No archaeopyle was seen.

FIGURED SPECIMEN: I.G.S. slide PK.107, sample WB 7 from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2834 ft 7 in. depth. Lower Kimmeridgian (Eudoxus Zone).

DIMENSIONS: Figured specimen: periblast length 105μ, breadth 76μ, endoblast length 80μ, breadth 70μ. Range: overall length 53–105μ, breadth 42–76μ, endoblast length 42–80μ, breadth 35–70μ. Measured specimens 5 in number.

OBSERVED RANGE: Lower to Upper Kimmeridgian (Mutabilis to Pectinatus).

REMARKS: Six specimens [two from the Lower Mutabilis, two from the Middle (Scitulus) and two from the Upper (Pectinatus) Kimmeridgian], all from English assemblages, were recorded. In general appearance, they are similar to *Dingodinium europaeum*, which was recorded from the Aptian of Germany by Eisenack (1958c). However, these specimens are larger; Eisenack did not record specimens over 65–67μ length. Since there is a very considerable stratigraphic gap and also a difference in dimensions, and in the absence of data regarding the archaeopyle, they were not placed in *D. europaeum* but were assigned to the genus *Scriniodium*.

Genus ***SIRMIODINIUM*** Alberti, 1961

Sirmiodinium grossi Alberti, 1961

Plate 16, figures 7–8

1961 *Sirmiodinium grossi* Alberti, 22, pl. 7, figs 5–7, pl. 12, fig. 5; table c.
1964 *S. grossi* Alberti; Downie & Sarjeant, 145.
1965 *S. grossi* Alberti; G. & M. Deflandre, fiches 2787–2788.
1966 *S. grossi* Alberti; Sarjeant, p. 212, pl. 22, fig. 7, table 5.
1967b *S. grossi* Alberti; Sarjeant, table 11.

DESCRIPTION: The cyst is dorso-ventrally flattened. The periblast is roughly pentagonal in shape, with a blunt apical horn and flattened antapex. The endoblast is subspherical to ovoidal, both ends rounded. The circular cingulum is very deep and divides the cyst unequally; the epitract is smaller than the hypotract. The tabulation is poorly indicated; on the dorsal side of the cyst, two apical, three precingular and three postcingular plates were recognised, but the ventral tabulation was not established. The surface of the endoblast is apparently smooth, the surface of the periblast minutely granular. In one of the five specimens observed, an apical archaeopyle was observed, formed by loss of the whole apex; in the other specimens, the apex is still attached to the shell in the position of the first apical plate and a median dorsal, precingular plate (possibly 3″) is also surrounded by splits, suggesting that a combination archaeopyle of an undescribed type is developed. In all the observed specimens there is a posterior dorsal aperture of circular shape.

FIGURED SPECIMENS: BM(NH) slide V.56373(1) and V.56374(1), sample CP 245, from the Rotunda Nodule Bed, Chapmans Pool, Dorset. Upper Kimmeridgian (Rotunda Zone).

DIMENSIONS: Range: overall length 65–80μ, length without apex 48μ, breadth 48–70μ, endoblast length 59–70μ, without apex 43μ, breadth 40–60μ. Measured specimens 5 in number. Holotype: overall length 91μ, breadth 86μ, endoblast length 72μ, breadth 61μ, as given by Alberti.

OBSERVED RANGE: Upper Kimmeridgian (Rotunda Zone).

TOTAL KNOWN RANGE: Upper Kimmeridgian (Rotunda Zone) to Upper Barremian.

REMARKS: Five specimens were observed, all from the same horizon in Dorset. These specimens are characterized by their archaeopyle formation and their posterior dorsal aperture. Alberti (1961) recorded the holotype from the Upper Hauterivian to Upper Barremian of Germany, Sarjeant (1966) encountered it also in the Lower Hauterivian. Its presence also in the Upper Jurassic suggests a direct relationship with *Scriniodinium*, from which it may well have evolved by enlargement of the archaeopyle.

Cavate cyst sp. indet A

Plate 16, figure 3

DESCRIPTION: The periblast is broadly ovoidal, with a well developed anterior pericoel. The endoblast is spherical. There are no apical or antapical projections; tabulations is not indicated. The relatively narrow cingulum divides the cyst unequally; the epitract is longer than the hypotract. The surface of the periblast is perforated; the endoblast has a granular surface. An archaeopyle was not observed.

FIGURED SPECIMEN: I.G.S. slide PK.102C, sample WB 2, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2959 ft 5 in. depth. Lower Kimmeridgian (Mutabilis Zone).

DIMENSIONS: Figured specimen: periblast length 63μ, breadth 52μ, endoblast length 48μ, breadth 49μ.

REMARKS: This observation was based on a single specimen. In its general shape, it looks similar to members of *Deflandrea* and *Hexagonifera*, but an archaeopyle was not observed. It may represent a new genus, but before this can be decided, better preserved specimens must be awaited.

Cavate cyst sp. indet. B

Plate 16, figures 2, 4

DESCRIPTION: The cyst is broadly ovoidal to elongate in shape, bearing a short, blunt, hollow apical horn, and one or two antapical horns. The endoblast is subspherical to spherical, with rounded ends. Tabulation and sulcus are not indicated. The broad cingulum divides the cyst unequally: the epitract is longer than the hypotract. The periphragm is densely perforated. The endophragm is smooth or minutely granular. An irregular breakage on the epitract, suggesting the beginning of opening of an apical or intercalary archaeopyle, was observed in some of the specimens.

FIGURED SPECIMENS: I.G.S. slide PK.104, sample WB 4, from Warlingham Borehole at 2910 ft 6 in. depth; and I.G.S. slide PK 106, sample WB 5, from the Borehole at 2885 ft 1 in. depth. Lower Kimmeridgian (Eudoxus Zone).

DIMENSIONS: Range (22 specimens were measured): overall length 45–70μ, breadth 33–60μ, endoblast length 33–53μ, breadth 31–50μ.

REMARKS: A group of specimens (44 in number), all from the Lower Kimmeridgian (Mutabilis to Pectinatus) of the Warlingham Borehole, were recorded which resemble, in their general appearance (with apical and antapical projections) the species of the genus *Deflandrea*. However, since no regular archaeopyle formation was observed, they are not attributed to that genus: they may indeed well be representatives of a new genus. The cavate cyst sp. indet. A (previously mentioned) shows similarities to these specimens, in their perforated periphragm and similar overall appearance, but has no projections at the apex and the antapex.

INCERTAE SEDIS

Group **ACRITARCHA** Evitt, 1963

Subgroup **ACANTHOMORPHITAE** Downie, Evitt & Sarjeant, 1963

Genus ***MICRHYSTRIDIUM*** Deflandre, emend. Sarjeant, 1967c

Micrhystridium recurvatum Valensi, 1953

Plate 17, figures 1–2

1953 *Micrhystridium recurvatum* Valensi, 43, pl. 6, figs 1–4, pl. 10, fig. 10.
1955 *M. recurvatum* Valensi; Valensi, 589, pl. 1, fig. 10.
1960c *M. recurvatum* Valensi; Sarjeant, 392, pl. 14, fig. 19, text-fig. 1a, table 2.
1962b *M. recurvatum* Valensi; Sarjeant, 489, text-figs 8b, f, tables 2–3.
1963 *M. recurvatum* Valensi; Wall & Downie, 778.
1964 *M. recurvatum* Valensi; Downie & Sarjeant, 133.
1964 *M. recurvatum* Valensi; Sarjeant, table 4.
1964 *M. recurvatum* Valensi; Gocht, 123, pl. 16, fig. 13, text-fig. 43.
1965b *M. recurvatum* Valensi; G. & M. Deflandre, fiches 2346–2351.
1965 *M. recurvatum* Valensi; Sarjeant, 177–178, pl. 1, figs 11–18, table 1.
1967 *M. recurvatum* Valensi; Dodekova, 27, pl. 3, fig. 10, table 1.
1967c *M. recurvatum* Valensi; Sarjeant, pl. 1, figs 1, 3–5, 9, text-fig. 1H.
1968 *M. recurvatum* Valensi; Sarjeant, table 2A.

DESCRIPTION: The cyst is spherical to subspherical, bearing simple, hollow, distally closed, curved processes, about 32–38 in number. The surface of the cyst is smooth or very finely granular.

FIGURED SPECIMEN: I.G.S. slide PK.127, sample WB 26, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2359 ft 9 in. depth. Upper Kimmeridgian (Pectinatus Zone).

DIMENSIONS: Figured specimen: diameter 10μ, process length 4μ. Range: diameter 13–20μ, process length 3–12μ, measured specimens 29 in number. Valensi gave the holotype diameter as 10μ, Sarjeant gave the mean diameters of the specimens from Normandy as 14μ. In contrast, Dodekova gave the average diameters of her Kimmeridgian specimens from Bulgaria as 22μ; these specimens appear well outside the normal size range and may well represent a distinct species.

OBSERVED RANGE: Lower to Upper Kimmeridgian (Cymodoce to Rotunda). Not yet observed from the Elegans and Scitulus Zones.

TOTAL KNOWN RANGE: Bajocian to Upper Kimmeridgian (Rotunda Zone).

Micrhystridium sp.

Plate 17, figures 7–8

1970 *Micrhystridium inconspicuum* Gitmez, pl. 1, fig. 8, table 4.

DESCRIPTION: A form of *Micrhystridium* having a spherical shell, with thick shell wall (c. 1μ). Processes are simple, conical, about 30 in number, and slightly curved.

The length of the processes is not more than one quarter of the shell diameter; they are hollow, distally closed, their cavity connected to the shell interior. The surface of the shell is smooth. An opening in the form of a split was observed in the single specimen seen.

FIGURED SPECIMEN: BM(NH) slide V.53953(1), sample OM 418, from 10 ft above the Ringstead Coral Bed, Osmington Mills, Dorset. Lower Kimmeridgian (Baylei Zone).

DIMENSIONS: Figured specimen: shell diameter 19 × 20μ, process length 4–5μ.

REMARKS: A single specimen recorded from the Baylei Zone of Dorset, was earlier placed into *M. inconspicuum* (Gitmez, 1970); subsequently, examination by high power objective has shown that it is different from *M. inconspicuum* as recently redefined by Deflandre and Sarjeant (1970).

With its short processes, this specimen is similar to the Oxfordian species *M. rarispinum* Sarjeant (1960c). However, its cyst diameter is greater than that of *M. rarispinum* and its processes are slightly longer and more numerous (Sarjeant gave the cyst diameter of the latter species as 11μ, process length 2–2·5μ and the process number as 14–20). It may represent a new species, but more specimens must be awaited.

Genus ***SOLISPHAERIDIUM*** Staplin, Jansonius & Pocock, 1965 emend. Sarjeant, 1968b

Solisphaeridium claviculorum (Deflandre) Sarjeant, 1968b

Plate 17, figures 9–10

1938e *Hystrichosphaeridium claviculorum* Deflandre, 191–2, pl. 10, fig. 4.
1963 *Baltisphaeridium claviculorum* (Deflandre); Downie & Sarjeant, 91.
1964 *B. claviculorum* (Deflandre); Downie & Sarjeant, 88
1964 *B. claviculorum* (Deflandre); Sarjeant, table 3.
1966 *B. claviculorum* (Deflandre); Davey, Downie, Sarjeant & Williams, 174.
1968 *?Solisphaeridium claviculorum* (Deflandre); Sarjeant, 233, pl. 2, figs 13, 15, table 2A.
1970 *S. claviculorum* (Deflandre); Deflandre & Sarjeant, 6, pl. 1, fig. 5.

DESCRIPTION: Cyst spheroidal, moderately thin-walled, bearing about 22 processes. These processes are simple and straight, their length about four-fifths of the cyst diameter; they are closed at both the distal and the proximal ends but contain an elongate cavity which does not connect to the central cavity of the shell. The surface of the cyst is finely granular. An opening, in the form of a split, was observed.

FIGURED SPECIMEN: I.G.S. slide PK.101, sample WB 1, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2984 ft 7 in. depth. Lower Kimmeridgian (Mutabilis Zone).

DIMENSIONS: Shell 18 × 20μ, process length 17μ. Holotype: overall diameter 58μ, process length 14–16μ (as given by Deflandre).

REMARKS: A single specimen of this species was originally recorded from the Upper Jurassic of France and attributed to the genus *Hystrichosphaeridium*. In 1963, Downie and Sarjeant transferred it to the genus *Baltisphaeridium* on the basis of its spine characters. Recently, one of the authors (W.A.S.S., 1968b), after re-examination of the holotype and recording further specimens from the Lower Oxfordian, placed this species in the genus *Solisphaeridium* hesitantly, because of the absence of clear knowledge of the mode of archaeopyle formation. Subsequent study of the holotype has since confirmed his judgement (Deflandre and Sarjeant, 1970).

A single specimen was observed in the Warlingham Borehole sample from the Mutabilis Zone which conforms in morphology to this species; since only one specimen was found, the presence of the species at this level, after such a stratigraphic hiatus, cannot be regarded as definite since pollution cannot be altogether ruled out.

Subgroup **NETROMORPHITAE** Downie, Evitt & Sarjeant, 1963

Organism A

Plate 16, figure 1; plate 17, figure 3

1970 Organism A Gitmez, 321, pl. 11, figure 9, table 4.

Description: The cyst is ellipsoidal to elongate. One pole is rounded, the other is flattened: the lateral walls are slightly outbowed. The cyst wall is thick (about 1μ), without ornamentation, processes or division into fields. The surface is smooth but porate; distribution of the pores is irregular, being generally densest around the flattened pole and on the sides of the cyst. An opening was observed in the flattened pole: its outline appears to be roughly circular.

Figured specimen: BM(NH) slide V.53948(3), sample RB 219, from the *Rhactorhynchia inconstans* Bed, Ringstead Bay, Dorset, Lower Kimmeridgian (Baylei Zone).

Dimensions: Figured specimen: cyst length 77μ, breadth 28μ. Range: length 42–77μ, breadth 18–48μ. Measured specimens 12 in number.

Remarks: This new form was observed in the assemblages from the Baylei and Mutabilis Zones of Dorset and Le Havre only. It resembles in general outline members of the genus *Palaeostomocystis*, especially the species *P. laevigata* Drugg, 1967 (Upper Cretaceous of California): but none of the specimens observed contains an internal cyst or sac-like body.

Subgroup **PTEROMORPHITAE** Downie, Evitt & Sarjeant, 1963

Genus ***PTEROSPERMOPSIS*** W. Wetzel, 1952

Pterospermopsis harti Sarjeant, 1960c

Plate 17, figure 6

1960c *Pterospermopsis harti* Sarjeant, 402–3, pl. 14, fig. 16, text-fig. 3, table 2.
1962b *P. harti* Sarjeant; Sarjeant, table 3.
1964 *P. harti* Sarjeant; Downie & Sarjeant, 143.

Figured specimen: I.G.S. slide PK.111, sample WB 8, from H.M. Geological Survey Borehole, at 2810 ft 6 in. depth. Lower Kimmeridgian (Eudoxus Zone).

DIMENSIONS: Figured specimen: overall 30 × 30μ, cyst 12 × 12μ. Overall dimensions of the other English specimen 32 × 32μ, cyst 17 × 17μ. French specimen: overall 30 × 30μ, cyst 12 × 12μ.

OBSERVED RANGE: Lower to Upper Kimmeridgian (Eudoxus to Pectinatus). (See below.) Total Known Range: Upper Oxfordian (Pseudocordata) to Upper Kimmeridgian (Pectinatus).

REMARKS: This species was originally recorded from the Corallian of Yorkshire. It is very rare in the Kimmeridgian, only three specimens being recorded, one each from France (Mutabilis), Warlingham Borehole (Eudoxus) and Dorset (Pectinatus Zone).

Subgroup **UNCERTAIN**

Acritarch sp. indet.

Plate 17, figures 4–5

DESCRIPTION: The cyst is elongate, ovoidal with rounded ends, bearing about 14–16 processes. These processes are simple, straight or slightly curved, conical and closed distally. The shell wall is composed of two layers, the outer layer forming the processes; the processes are hollow but their cavities are not in contact with the central cavity. The surface of the cyst is smooth or minutely granular. An irregular opening was observed.

FIGURED SPECIMENS: I.G.S. slides PK.125 and PK.126, sample WM 26, from H.M. Geological Survey Borehole, Warlingham, Surrey, at 2359 ft 9 in. depth. Upper Kimmeridgian (Pectinatus Zone).

DIMENSIONS: Range: Shell length 15–35μ, breadth 8–15μ, process length 6–10μ. Measured specimens 5 in number.

REMARKS: All the specimens were recorded from the same horizon in the Warlingham Borehole (Pectinatus Zone). They differ from described species in their elongate shape and irregular opening. They may represent a new species and perhaps even a new genus.

IV. STRATIGRAPHICAL DISTRIBUTION CHARTS

See Tables 3 to 6.

V. CONCLUSIONS

In the Kimmeridgian samples from England, Scotland and France described by Gitmez (1970) and herein, 36 genera, comprising 110 species, of dinoflagellate cysts and 6 genera, comprising 16 species, of acritarchs were recognised. From these, two new genera, 23 new species and 4 new varieties have been proposed: more than a dozen other forms certainly represent new species but were not proposed as such, because of poor preservation or (more frequently) inadequate numerical representation. In addition, there was a further list of species, probably new, whose preservation, presentation or orientation entirely precluded their description: the microplankton of the Kimmeridgian Stage is thus much more rich and more varied than has hitherto been recognised.

TABLE 3

The numerical distribution of microfossils in the Kimmeridgian assemblages from Dorset, Oxfordshire, Cambridgeshire and Scotland (Staffin Bay and Cromarty)

	DORSET																					CAMBS	OXFORDSHIRE			SCOTLAND			
	Baylei Zone							Autissiodorensis Zone			Elegans Zone	Scitulus Zone	Wheatleyensis Zone		Hudlestoni–Pectin	Pectinatus Zone				Rotunda Zone		Baylei Zone	Pallasioides Zone			Baylei Zone			Cymodoce Zone
	OM 131	OM 418	OM 419	OM 420	HD 191	RB 218	RB [illegible]	KD [illegible]	KD [illegible]	KD [illegible]	KD 227	CD 229	CH 231	RD 234	FD 236	FD 237	ED 240	LD 242	HC 243	CC 245	HC 246	[illegible] 444	LO 352	LO 353	LO 360	SS 625	SS 626	SS 627	CS 421
Chytroeisphaeridia chytroeides	21	17	14	16	.	.	.	24	.	14	3	1	6	2	28	4	1	24	17	77	13	18	4	.		17	11	8	[illegible]
C mantelli	.	.	.	2	.	.	.	.	.	.	.	.	10	.	.	.	2	2	.	.	.								
C pococki	10	3	1	1	.	.	.	5	.	51	9	.	4	.	16	.	11	8	12	3	.	1	3	1		5			1
Fromea warlinghamensis	.	.	.	.	.	.	.	.	.	.	.	.	24	.	.	.	1	.	.	.	.	.	.	1					
Tenua capitata	.	.	1	.	.	1	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.							3
T echinata	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	3	1	.	.	.	1	2	.	.	.		
T hystrix	15	3	1	1	.	1	9	.	.	.	.	.	4	.	4	1	.	11	19	.	.	12	11	27	.	5	1	1	35
T pilosa	10	1	3	.	.	.	7	.	.	.	.	.	.	.	3	.	.	6	7	.	.	9	1	2	.	4	2		1
T sp	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	
Acanthaulax venusta	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.						
Cryptarchaeodinium calcaratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	1	1	.						1
C cf calcaratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.						
Gonyaulacysta aculeata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.						
G angulosa	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.						
G cauda	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.							
[illegible]							.												2			1	2			4	4	.	
[illegible]	4																												
[illegible]	2																		1										
[illegible]	.	.										3							1										
G granulata	.	3	2	2	2	7	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.				1
G granuligera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	.	.			.		.	
G cf helicoidea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	11	3
G hyaloderma	3	3	6	20	1	49	63	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.		
G jurassica	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	.	
G jurassica var. longicornis	.	.	.	.	.	.	.	.	.	3	6	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
G longicornis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	
G cf mamillifera	2	3	2	1	1	.	11		16	16	5	3	3		13	2	19	4	2	1		4		4	.	1	.	1	5
G nuciformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	4	3	1	.	1	.	.	1	.	.	
G perforans	1	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.					
G serrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8					
G sp A																													
G sp D																			1										
G sp F	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	.	2	.										
G sp G	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.									
G sp H	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1							
Leptodinium aceras	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.							
L amabilis	2	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4					
L arcuatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.						
L cf crassinervum	10	6	1	.	2	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.						
L egemenii	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	6	.	.						
L cf subtile	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.							
L sp.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.							1
Occisucysta balios	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		.	.
O monoheuriskos	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
O sp (Gitmez, 1970)	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1
Belodinium dysculum	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Dictyopyxis areolata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
D cf reticulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.					3					
Histiophora cf. ornata	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.							3			1
Meiourogonyaulax dicryptos	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.	.	.	2	1						[illegible]			
M pila	3	.	.	.	1	.	5	.	.	.	.	.	.	.	.	.	.	.	.										
M. staffinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				1						
M sp A (Gitmez, 1970)	.	.	.	.	.	.	.	.	.	.	.	.	1	.	4	.	.	3	2			1	1						2
M sp B, herein.	.	.	.	.	.	.	5	1	1	3	.	.	.	.	.	.	.	.	.	.	.								
Apteodinium granulatum	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	2	.	.	.	.	10	2	11	.	3	1	1	[illegible]
A cf maculatum	8	5	4	5	.	5	13	18	.	23	5	5	2	.	10	2	5	14	21	2	1	.	.	.	.	.	.	.	
Pareodinia ceratophora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	2	1	.	.	.	.	.	.	1
Trichodinium sp	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	
Imbatodinium antennatum	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	.	.	
I cf villosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Nannoceratopsis pellucida	2	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	8	5	.	.	.	.	.	.	.	.	.	
Egmontodinium polyplacophorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	1
Proximate cyst sp indet.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	
Heslertonia pellucida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	
Epiplosphaera reticulospinosa	2	1	1	1	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	1	3	.	.	.	.	
Adnatosphaeridium paucispinum	6	1	.	.	.	5	2	1	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	
Cleistosphaeridium ehrenbergi	1	1	.	.	.	5	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	
C polyacanthum	2	.	1	1	.	1																							
C polytrichum	4	1	1	.	.	11	8											.	1	.	.	.							
C tribuliferum	.	.	.	1	.	.												21	5	.	.	.							
C sp (Gitmez, 1970)																								1		2	6	3	
C sp., herein	.	.	.	.	.	26	2	.	.	.	.	.	.																
Hystrichosphaeridium petilum	2	.	2	.	.	.	2	.	.	.	.	.	.																
Oligosphaeridium pulcherrimum	.	.	.	.	.	2	.	.	.	.	.	.																	
Polystephanephorus sarjeantii		1																								2	6	3	1
Prolixosphaeridium cf deirense															1			1	2		1	3	1	1		2			1
P granulosum	7	1	1		1	19	1														2	6	4			5	2	9	3
P. parvispinum				2			1								5	3	-	5	6				1	30		4	1		
Systematophora areolata	1	6	7	5		2	4			1			4		10		52	26	9					1					1
S orbifera	1	13	3	2		1													3			.				3			
S. ovata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			3	
Taeniophora iunctispina	2	.	2	.	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
Stephanelytron cf scarburghense	5	2	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.				
Endoscrinium cf campanula	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.		1
E galeritum	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	3	1	.	.
E luridum	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	3
E oxfordianum	1	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	3	1	.	1	.	4	.	.	.	.	.
Psaligonyaulax apaleta	1	.	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	.	.	22
P sp (Gitmez, 1970)	.	.	.	1	.	.	.	.	.	.	.	.	.	.	23	.	.	3	4	4	4	3	1	4	.	1	.	.	1
Hexagonifera jurassica	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	1	.	.	.	4	.	.	.	.	
Iarvocavatus tuberosus	.	1	.	2	.	.	.	.	.	.	.	.	.	.	2	.	1	15	10	1	.	.	.	.	.	1	2	2	
Scriniodinium bicuneatum	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
S. crystallinum	3	3	.	3	.	8	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	
S. dictyotum subsp dictyotum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.			
S. dictyotum subsp osmingtonensis	3		2	1																									1
S. dictyotum subsp papillatum			1	3			1																						
S dictyotum subsp pyrum		1	1	1			1								3		1												
S playfordi		1	1										1							5									4
S sp															2			2											
Sirmiodinium grossii	14	6	4	8	1					2																			
Netrelytron parum	12																										1	5	12
N stegastum				1									1		4	2		1	1	50	1	25		1				2	43
Baltisphaeridium [illegible]	1	7	2	6	1	11	9	7												27		80	2						1
Micrhystridium fragile		4	1	4	1	1																							
M inconspicuum								1														18		3				3	
M recurvatum				1		1																							
M sydus																			2										
M sp		1																				-		9		1	1	1	30
Solisphaeridium brevispinosum	3			1		36	22		2		1		1		3	2			7	59	4								
S stelliferum	11	6	4	9																		10						1	4
Organism A		1		1			11												2							1		1	
Veryhachium hyalodermum	5						17	1		6	4							1				1	1			0			4
Staphinium cistum					1											1													1
Pterospermopsis australiensis					.	.																1							
P harti																													
P helios																													
Total number of determined microplankton	202	104	84	108	12	215	225	60	20	127	17	25	64	2	165	41	112	174	183	249	47	224	51	159	-	84	50	75	214
Indeterminate microfossils	98	50	69	51	40	89	116	53	30	171	25	33	90	6	130	41	142	115	142	56	30	92	60	159		65	43	60	100
Foraminiferal shell linings	.	.	5	1				8		10	12		1		5	2	1	6	1			9	3	1		13	3	4	
Pollen & Spores	39	13	27	6	18	41	213	74	67	33	80	73	81	92	81	86	66	48	77	95	84	45	48	56	38	40	70	56	103
Wood fragments	3						5	4			4	2	1	1	1		6	8	6	1	8		8	3	7	4	4	1	
TOTAL	342	167	185	166	70	345	559	199	123	344	138	133	237	101	388	150	347	351	409	401	169	370	182	378	45	206	176	202	423

TABLE 4

The numerical distribution of microfossils in the Kimmeridgian assemblages from the Warlingham Borehole, Surrey

	Mutabilis Zone			Eudoxus Zone								Autissiodorensis Zone			Elegans Zone	Scitulus Zone		Wheatleyensis Zone		Hudlestoni Zone			Pectinatus Zone				Rotunda Zone		
	WB 1	WB 2	WB 3	WB 4	WB 5	WB 6	WB 7	WB 8	WB 9	WB 10	WB 11	WB 12	WB 13	WB 14	WB 15	WB 16	WB 17	WB 18	WB 19	WB 20	WB 21	WB 22	WB 23	WB 24	WB 25	WB 26	WB 27	WB 28	WB 29
Chytroeisphaeridia chytroeides	33	11	49	61	42	94	39	23	[illegible]	62	31	[illegible]	[illegible]	[illegible]	31	[illegible]	[illegible]	14	[illegible]	5	3	17	[illegible]	27	35	37	9	17	7
C. mantelli	.	.	.	.									4	[illegible]	5			1								[illegible]			
C. pococki	2	2	6	3	7	.	7	8	5	17	12	5	10	.	[illegible]	23	[illegible]	.	1	[illegible]	.	4	8	11	3	1	3	3	1
Fromea warlinghamensis	.	.	.	.	.	.		.	.	.	.	.	1	1															
Tenua capitata	.	2	.	.	.	.	.			.	.	.	.	.	.	.	.	.	.	.		.							
T. echinata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.													
T. hystrix		2	.	3	.	.	.	.	.	.	.	.	.	.	.	1		.	.	2	.	.	1						
T. pilosa	.	6		.	.		.	.	.	.	.	.	.	.	.	10	4	.	8	8	.	.	1	.					1
Gonyaulacysta angulosa	.		.	.	.			.	.	.	.	.	.		.	.	.	.	2	3									[illegible]
G. cladophora	.	.	.	.	.	.	1		.	.	.	.	.	.	.	.	.	.	.	.	.	.	2						1
G. ehrenbergii										.	.	.																	
G. cf. giuseppei	.	3	.		.	.	.								.														
G. globata	.	.					.	.	.	.																			
G. granulata	1	2	1	2	.	.	1	.		.	.	.	2	.	1					3									
G. granuligera	.	.	.	.	.	.	.			.	.	1			1			1	1										1
G. jurassica	1	.	1	.	.	.	.	2																					
G. jurassica var. longicornis	.	.	.	.	.	.		1																					
G. longicornis	1	1																											
G. cf. mamillifera	.	.	.	.	.	.								.	3		5		1	1		1	3						
G. nuciformis	6	.	.	.	.	.	5	2	7	.																			1
G. perforans	.	.	.	.	.		.		.	.					.		8	[illegible]		.				1					2
G. sp. B	.	.	.		.	.	.	.	.	.	.	.	.	.	1	.				5		.				1			5
G. sp. C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1													
G. sp. E	.	.	.	.	.	.	.	.	.																				
Leptodinium aceras	.	.	.	.		.	2	.	1				.																
L. arcuatum	.	.	.	.	.								1										1						
L. sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.										
Occisucysta balios	.	5	.	.	.	.	.													1				1					
Histiophora cf. ornata																													
Meiourogonyaulax pila	.	.																											
M. stalfinensis	.	.	.	.	.		1												1										
M. sp., herein	1	.																											1
Apteodinium granulatum	.	.	.	.	.	.	.	.	.	.	.	.	1		.	3	.			3									
A. cf. maculatum	.	.	.	1	.	.	.	.	.	.	.	.	.																
Pareodinia ceratophora	5	6	4	2	3	.	.		.	1	1	.	7			.	.	5		3			3	.		1			1
Imbatodinium antennatum	.	.	.	.	.	.		.	.	.	1	.	.	.		.	1						5						
Proximate cyst sp. indet.	.																												11
Cleistosphaeridium ehrenbergi	2	3	.																										1
C. polyacanthum	.	.	.	1																									
C. tribuliferum	.	1	.	.	.	.	.																						
C. sp., herein	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.		.	.	.	2					
Hystrichosphaeridium petilum	.	3	.	.	.	.	.	.	.	.	.	.	.	.															
Prolixosphaeridium granulosum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1										
P. parvispinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1											
Systematophora areolata	.	23	.	2	.	.	.	.	.	.	.	.	6	1	.	.	.	.	4	3	.	.	.	.					
S. orbifera	.	2	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	1	.	.	.	.	.	.	2		
Endoscrinium luridum	.	.	.	1	1	.	.	.	.	.	.	.	.																
E. oxfordianum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	2	.	.	.	.	.	.	.			
Psaligonyaulax apaleta	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1		2
Hexagonifera jurassica	.	.	.	1	5	.	.	.	.	.	.	.	1	.	.	.	.	.	24	7	.	.	.	1	1	.	3	2	[illegible]
Parvocavatus tuberosus	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1														
Muderongia simplex	.	.	.	.	.	.	.	.	.	.	.	.	.																11
Scriniodinium bicuneatum	.	1	.	.	.	.	.	2	.	.	.	.	3	.	.		.	4	.	7									2
S. crystallinum	1																												
S. dictyotum subsp. papillatum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.						
S. playfordi	2	.	.	.	.	.	.	1	.	.	.	.	1		2	1	.	.	.	.	.	.	.	1					[illegible]
S. sp.	.	.	.	.	.	.	1	.	.		.	.	.	1	.	1	.	.	.	.	.	.	.	.	1				
Netrelytron parum									1																				
Cavate cyst sp. indet. A																											.		
Cavate cyst sp. indet. B	.				[illegible]																			1					
Micrhystridium fragile	66	5	9	[illegible]	[illegible]											3		11	1	.	.	.	1	.	.	11	[illegible]		.
M. inconspicuum	2	.		3																						[illegible]	3	.	
M. recurvatum	7	2	1	.	.	.	.	.	.	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	1	11	.		
M. sydus	.	.	.	2	1	.	1	.	.		.	.	.	.	1	.	.	.	.	.	.	.	.	.		1	1	.	
Solisphaeridium claviculorum	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		.			
S. stimuliferum	25	5	11	9	1	.	.	.	.	1	.	.	2	.	2	1	.	.	.	.	.	.	1	.	.	.	[illegible]	[illegible]	[illegible]
Veryhachium hyalodermum	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	1	27	38	[illegible]	3
Pterospermopsis australiensis	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		.
P. harti	.	.	.	.	.	.	.	1																					
Acritarch sp. indet.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.
Total number of determined microplankton	158	93	84	101	119	95	61	40	43	81	47	32	101	72	88	112	52	49	87	65	10	24	56	47	42	97	80	39	[illegible]
Indeterminate microfossils	41	115	25	16	17	7	48	61	57	18	22	17	108	33	117	45	106	50	118	153	20	32	53	34	7	20	27	27	[illegible]
Foraminiferal shell linings	1	.	.	.	.	3	2	10	6	10	.	13	.	.	.	.	.	1	.	.	1	.	.	3	.	.	.	.	
Pollen & Spores	88	60	94	94	91	83	75	43	58	83	81	84	72	70	67	80	58	83	75	62	82	82	77	77	93	92	92	94	[illegible]
Wood fragments	3	12	1	.	.	1	4	18	12	2	3	5	.	1	1	.	1	2	.	6	.	7	2	11	1	.	1	1	.
TOTAL	291	280	204	211	227	189	190	172	176	193	151	132	281	176	274	[illegible]	[illegible]	185	290	286	113	145	188	172	143	209	200	161	[illegible]

TABLE 5

The numerical distribution of microfossils in the Kimmeridgian assemblages from France

	Baylei Zone											Cymodoce Zone					Mutabilis Zone					Autissiodorensis Zone				Scitulus Zone	Pallasioides Zone
	Boulonnais							Normandy	Le Havre		M Crussol	Normandy	Lorraine	Mont Crussol			Le Havre	Jura Mountains				Mont Crussol				Boulon.	Jura M
	CC 447	CC 448	CC 449	CC 450	CC 451	CC 452	CC 455	VN 184	HF 185	HF 186	MR 547	BN 179	L [illegible]	MR 548	MR 549	MR 550	HF 395	OF 485	OF 486	OF 487	BV [illegible]	MR 552	MR 553	MR 554	MR 555	CC 453	MV 489
Chytroeisphaeridia chytroeides		5						11	[illegible]	25							6	[illegible]	3		[illegible]					60	5
C mantelli																	5										
C pococki			1						1	1								5	1		5						
Tenua capitata		1	1						1																		
T echinata												1															
T. hystrix		1	5	1		2	1	5	6	3		3							1								
T pilosa									1			8						1									
Acanthaulax venusta								1																			
Cryptarchaeodinium sp				1																							
Gonyaulacysta aculeata	2							1	1																		
G angulosa			1		1		1	1																			
cauda	1																										
G cladophora	1											5															
G ehrenbergii	2	1						2																			
G eisenacki																											
G cf eisenacki				3																							
G cf giuseppei		1																									
G granulata	2	2		8		1	1			1		1							3								
G granuligera	3	4	3	16	1	6	1	2					1														
cf helicoidea								1																			
hyaloderma								1																			
jurassica	2	4		5	1			[illegible]				[illegible]															
jurassica var longicornis				3								10															
longicornis	6		3	2																							
G cf mamillifera	1																										
nuciformis	1			9	1	8	1	1		1	1						2		4								
G serrata								2	1																		
G systremmatos	6																										
G sp A								1																			
Leptodinium amabilis									1																		
L arcuatum		1				1		1																			
L clathratum				1																							
L. egemenii									9	3		3															
L cf subtile												1															
Occisucysta balios	1			1				2																			
Dictyopyxis areolata			1						2								1										
D cf reticulata												1						4	4								
Histiophora cf ornata	1		1																								
Meiourogonyaulax dicryptos												1															
M staffinensis	1			6			1	1				2						3									
Apteodinium granulatum				5	1																						
A cf maculatum				1																							
Pareodinia ceratophora		14		5					14																		
Imbatodinium antennatum			1																								
Heslertonia pellucida												1	1				1										
Epiplosphaera reticulospinosa																											
Adnatosphaeridium paucispinum												9															
Cleistosphaeridium ehrenbergi	3								2			4					1				3						
C polyacanthum	2								5																		
C tribuliferum												2															
C sp (Gitmez, 1970)		1						1	1																		
Hystrichosphaeridium petilum	1							6				1									1						
Oligosphaeridium pulcherrimum			2																								
Polystephanephorus sarjeantii	1																										
Prolixosphaeridium granulosum	1							1	4			1	1				1				2						
Systematophora areolata	75	5	6	14	12	15		51	6	6	1	13					1	34	2		6						
S orbifera	33	3	5	4	3	13		3																			
Taeniophora iunctispina	4	1			3	1		3	2	1		9															
Stephanelytron redcliffense												5															
S cf redcliffense																											
S scarburghense							1		1	1																	
Endoscrinium cf campanula	4	4	1	3																							
galeritum	2																										
luridum	1						1	2										1									
E oxfordianum								3	1																		
E sp																		1									
Psaligonyaulax apaleta	2	1		3				2	2	1											4						
Hexagonifera jurassica			1					3	2								9										
Parvocavatus tuberosus	1	22	1	5	1					24																	
Scriniodinium bicuneatum	4										1																
S crystallinum		1			1		3	1	3			17															
S dictyotum subsp papillatum										1																	
S dictyotum subsp pyrum		2							1	1																	
S cf galeatum		1																									
S playfordi	4								1								6										
Netrelytron parum		1	12	4	1			6	1	2																	
N stegastum									3																		
Baltisphaeridium inusitatum								1																			
Micrhystridium fragile	4	5	1	4	2	5		8				17	4				4										
M inconspicuum	1							2	12			1					22										
M recurvatum											2	17					4										
M sydus									4				1														
Solisphaeridium brevispinosum									3																		
S stimuliferum	32	17	4	4	54		2	24	15	1	1						37				5						
Organism A									2																		
Veryhachium hyalodermum								1									1										
Staplinium cistum												18					103		1	1							
Pterospermopsis australiensis																	2										
P harti																				1							
P. helios													1				1										
Total number of determined microplankton	207	87	56	110	82	60	13	168	181	93	7	215	18				232	77	32	2	126					60	5
Undetermined microfossils	107	126	81	188	48	122	29	133	120	50	18	87	42				64	80	64	7	43	1				20	
Foraminiferal shell linings		3	3	10	4	1											4	129	1	2	2						
Pollen & Spores	8	16	1	21	12	21	72	10	27	20	54	65	124				77	35	60	84	52	9	17	13	11	400	[illegible]
Wood fragments		3										1	12				1	10	11	9	1						16
TOTAL	322	235	141	329	146	204	114	311	328	163	79	368	196	—	—	—	378	334	168	104	223	10	17	13	11	480	104

TABLE 6

The distribution of Kimmeridgian microplankton comparing with their previously known stratigraphic range

	Kimmeridgian																			Previously known stratigraphic range						
	Baylei Zone			[illegible] Zone		Eudoxus Zone	Mutabilis Zone		Autissiodorensis Zone		Elegans Zone	Scitulus Zone		Wheatleyensis Zone	Hudlestoni Zone	Pectinatus Zone	Rotunda Zone	Pallasioides Zone								
	England	Scotland	France	Scotland	France	England	England	France	England	France	England	England	France	England	England	England	England	England	France	Pre-Callovian	Callovian	Oxfordian	Kimmeridgian	Portlandian (Tithonian, Volgian)	Lower Cretaceous (Berriasian-Valanginian)	Post Valanginian
Chytroeisphaeridia chytroeides	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x		x	x	X	X	X				
C. mantelli	x	x	x	x	x	x	x	x	x		x	x				x	x		x	X						
C. pococki	x	x	x	x		x	x	x	x		x	x		x	x	x	x	x	x		X					
[illegible] warlinghamensis									x			x				x										
Tenua capitata	x		x	x			x															X	X			
T. echinata	x				x	x						x		x			x	x								
T. hystrix	x	x	x	x	x	x	x		x			x		x		x	x	x	x							X
T. pilosa	x	x	x	x	x							x		x		x	x	x			X	X				
T. sp.	x	x			x			x	x			x			x	x				X	X					
Acanthaulax venusta	x	x	x	x	x			x		x		x	x				x		x		X	X	X			
Cryptarchaeodinium calcaratum	x	x	x	x		x	x		x	x		x	x	x		x	x						X			
C. cf. calcaratum		x	x	x		x	x		x	x	x	x	x	x		x										
C. sp. (Gitmez, 1970)		x	x	x				x	x	x	x	x	x	x	x	x										
Gonyaulacysta aculeata	x		x																			X	X			
G. angulosa	x		x		x							x														
G. cauda	x		x																							
G. cladophora	x	x	x		x															X	X	X	X			
G. ehrenbergii			x																							
G. eisenacki	x				x				x	x	x	x					x		x	X	X	X				
G. cf. eisenacki	x		x	x					x	x	x										X		X	X		
G. cf. giuseppei	x	x	x		x		x			x	x	x	x					x	x	X	X					X
G. [illegible]														x	x											
G. [illegible]	x		x		x		x		x		x	x		x	x	x	x					X	X			
[illegible]	x		x		x				x		x					x	x	x					X			
G. cf. helicoidea	x	x	x													x	x									X
G. hyaloderma		x	x																				X			X
G. jurassica	x	x	x	x					x												X	X	X			
G. jurassica var. longicornis	x	x	x		x				x													X				
G. longicornis			x				x		x					x									X			
G. cf. mamillifera			x														x						X			
G. nuciformis	x	x	x								x					x					X	X				
G. perforans	x		x				x									x	x	x						X		X
G. serrata	x	x	x	x	x	x		x	x		x	x	x	x	x	x	x	x	x	X	X			X	X	X
G. systremmatos			x																							X
[illegible]	x		x																							
[illegible]												x														
[illegible]																		x								
[illegible]																x										
G. sp. II	x													x												
Leptodinium aceras		x	x	x	x	x			x			x		x		x										X
L. amabilis	x		x		x	x		x								x							X			
L. [illegible]	x		x						x							x						X				
L. [illegible]																								X		
L. [illegible]																		x					X			
L. [illegible]	x	x	x		x									x												
L. cf. subtile	x	x		x	x		x	x	x	x		x	x	x	x	x		x	x	X	X	X				
L. sp.		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x								
Occisucysta balios	x	x	x			x	x			x	x	x	x	x	x	x	x									
O. monoheuriskos	x	x	x	x	x	x	x	x	x	x		x		x		x	x									
O. sp. (Gitmez, 1970)	x																									
Belodinium dysculum	x	x	x																					X		
Dictyopyxis areolata	x	x	x	x				x														X	X			
D. cf. reticulata		x	x	x	x			x												X						
Histiophora cf. ornata	x		x											x									X			
Meiourogonyaulax dicryptos			x	x	x									x	x	x	x									
M. pila			x	x		x	x	x				x		x			x									
M. staffinensis	x	x	x	x	x	x		x		x		x	x	x	x	x	x	x								
M. sp. (Gitmez, 1970)		x	x		x	x	x				x	x	x	x					x							
M. sp., herein	x	x	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x							
Apteodinium granulatum	x	x	x	x										x			x	x								X
A. cf. maculatum	x	x	x			x		x				x			x	x										X
Pareodinia ceratophora	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x		X	X	X			X	
Trichodinium sp.	x		x	x	x		x	x		x	x	x					x	x	x							
Imbatodinium antennatum	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x				X		X		X	
I. cf. villosum	x	x			x	x	x	x			x	x	x	x		x	x	x		X	X	X	X	X	X	X
Cannosphaeropsis pellucida	x		x	x	x			x		x	x	x		x			x	x	x	X	X	X	X	X	X	X
Egmontodinium polyplacophorum	x	x	x		x	x	x	x		x	x	x		x		x										
Proximate cyst sp. indet.	x		x	x			x	x		x	x	x	x	x	x	x	x									
Heslertonia pellucida	x	x	x	x	x		x	x		x	x	x				x										
Epiplosphaera reticulospinosa	x		x					x								x							X			
Adnatosphaeridium paucispinum					x										x							X				
Cleistosphaeridium ehrenbergi	x	x	x		x		x	x								x	x	x			X	X				
C. polyacanthum	x		x																							
C. polytrichum	x					x										x				X	X	X	X			X
C. tribuliferum	x	x			x		x									x						X				
C. sp. (Gitmez, 1970)	x															x										
C. sp., herein											x					x	x									
H[illegible]	x	x	x		x		x	x										x								
Oligosphaeridium pulcherrimum	x		x																						X	X
Polystephanephorus sarjeantii	x		x																							X
Prolixosphaeridium cf. deirense	x																									X
P. granulosum	x	x	x	x	x		x	x				x		x		x	x	x				X	X			X
P. parvispinum	x	x		x										x				x				X				X
Systematophora areolata	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x					X			
S. orbifera	x	x	x				x					x		x	x	x	x	x				X	X			
S. ovata	x			x												x		x				X	X			
Taeniophora iunctispina	x	x	x	x	x																	X				
Stephanelytron redcliffense	x	x	x	x	x																				X	
S. cf. redcliffense					x																	X			X	
S. cf. scarburghense	x	x	x																			X			X	
Endoscrinium cf. campanula	x	x	x													x				X	X	X	X	X	X	
E. galeritum	x		x												x					X	X	X	X		X	
E. luridum	x	x	x					x														X	X		X	
E. [illegible]	x	x	x								x	x		x	x	x		x				X	X		X	
E. sp.								x					x									X	X		X	
Psaligonyaulax apaloba	x		x	x				x	x				x	x	x		x	x					X		X	
P. sp. (Gitmez, 1970)	x												x					x					X		X	
Hexagonifera jurassica	x	x	x			x			x				x	x	x	x	x	x					X		X	
[illegible]	x	x	x	x			x	x			x		x		x	x	x	x					X		X	X
Muderongia simplex	x	x											x		x		x					X	X		X	
[illegible]	x		x	x	x		x		x					x		x	x	x				X	X		X	
S. crystallinum	x	x	x		x		x						x		x	x							X	X	X	
S. dictyotum subsp. dictyotum	x	x											x		x	x		x							X	
S. dictyotum subsp. osmingtonensis	x	x													x	x		x							X	
S. dictyotum subsp. papillatum	x	x	x				x						x		x	x		x							X	
S. dictyotum subsp. pyrum	x	x	x										x		x	x									X	X
S. cf. galeatum	x	x	x										x		x	x							X	X	X	
S. [illegible]	x					x	x		x		x	x	x	x	x	x	x	x							X	
S. sp.	x					x	x		x			x	x	x	x	x		x							X	X
[illegible]															x	x	x	x							X	
Netrelytron pirum	x		x	x		x	x		x						x	x	x	x				X			X	
N. stegastum	x		x															x								
Cavate cyst sp. indet. A							x																			
Cavate cyst sp. indet. B						x	x					x				x							X			
[illegible]	x		x																							X
Micrhystridium fragile	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x		X	X	X				X
M. inconspicuum	x	x	x	x	x	x	x	x	x							x	x			X	X	X	X			
M. recurvatum				x	x	x	x		x							x	x			X		X				
M. sydus	x	x	x			x		x	x		x					x	x									
M. sp.	x																				X	X				
Solisphaeridium brevispinosum	x		x													x						X				
S. [illegible]							x													X	X	X				
S. stimuliferum	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x								
Organism A	x		x					x																		X
Veryhachium hyalodermum	x	x	x	x			x	x	x		x					x	x	x								
[illegible]	x	x			x			x	x		x														X	X
Pterospermopsis australiensis	x	x		x		x	x	x	x							x	x	x				X				
P. harti						x		x								x					X					
P. helios	x			x				x		x						x										
Acritarch sp. indet.																x										

The assemblages are dominated by proximate cysts, of which 68 species have been described. *Gonyaulacysta* is the dominant genus, represented by 29 species and some 800 specimens. The most abundant species is *G. jurassica* (301 specimens); this is, however, confined to the Lower Kimmeridgian, predominating in the Baylei and Cymodoce Zones and occurring only sparsely in the higher zones of the Lower Kimmeridgian. It has already been shown to be present in the Lower and Middle Callovian and abundant in the Lower Callovian and Oxfordian: its frequency makes it a useful stratigraphic index for these two stages and part-stage. *G. nuciformis*, represented by 184 specimens, ranges throughout the Kimmeridgian and has been previously recorded from Upper Callovian and Oxfordian: its presence or absence in the Portlandian remains to be elucidated. Three other species, *G. longicornis, G. granulata* and *G. granuligera*, are each represented by 50–55 specimens; *G. granulata* occurs in the uppermost Oxfordian also, the remaining two species being only recorded from the Kimmeridgian. The two latter species are most abundant in the Lower Kimmeridgian, though ranging throughout the stage. *G. longicornis* has a more uneven distribution: it is infrequent in the Lower Kimmeridgian, attains maximum frequency in the Middle, and was encountered only in the topmost (Pallasioides) zone of the Upper Kimmeridgian. *G. perforans* occurs in the Middle and Upper Kimmeridgian in sufficient numbers to serve as a useful index for those levels: other species with restricted ranges are numerically less frequent. Four other tabulate genera with precingular archaeopyles, *Leptodinium, Acanthaulax, Cryptarcheodinium* and *Occisucysta*, are also well represented.

Proximate cysts with apical archaeopyles (genera *Tenua, Chytroeisphaeridia, Fromea, Egmontodinium, Dictyopyxis, Meiourogonyaulax*) are much less important. *Meiourogonyaulax* ranges throughout the Kimmeridgian: the high-crested species *M. staffinensis* is especially conspicuous and a good index fossil. *Dictyopyxis* was not encountered higher than the Lower Kimmeridgian: the other genera appear less useful as stratigraphic indices. Two genera of proximate cysts with intercalary archaeopyles, *Pareodinia* and *Imbatodinium*, are present: the former is long-ranging, but the latter (known to date only from the Kimmeridgian) is potentially important. Proximochorate cysts were poorly represented by only two genera: the absence of *Spiniferites* is noteworthy and suggests that prior records from the Oxford and Kimmeridge Clays were a product of contamination.

Chorate and cavate cysts were present in comparable numbers (19 and 21 species respectively). Chorate cysts with complex process groupings (*Systematophora, Polystephanephorus, Epiplosphaera* and *Taeniophora*) are characteristic, the two latter genera being encountered only in the Lower Kimmeridgian. *Stephanelytron*, hitherto known only from the Oxfordian, ranges only as high as the Cymodoce Zone and appears an important index. The long-ranging genus *Prolixosphaeridium* may repay fuller study, since the circumscription of the species erected to date appears most unsatisfactory. *Cleistosphaeridium* is abundant throughout: in contrast, the two species with tubular spines both had only a sparse representation.

Of the cavate cysts present, *Endoscrinium* and *Scriniodinium* (both abundant in the Oxfordian) dwindle in importance markedly after the Lower Kimmeridgian. *Netrelytron, Psaligonyaulax* and *Hexagonifera* range throughout the stage, the former consistently in low numbers: *Muderongia* and *Sirmiodinium*, characteristically Lower Cretaceous, enter only in the uppermost zones.

Acritarchs are only a minor constituent of these assemblages and consistently occur only in low numbers. Acanthomorphs are the most numerous acritarchs, especially the various species of *Micrhystridium* and *Solispheridium stimuliferum*: pteromorphs, prismatomorphs, netromorphs and polygonomorphs are also infrequently present.

The stress of this study was placed on the lower zones of the Kimmeridgian and the horizons of the Middle and Upper Kimmeridgian require further study before a full stratigraphical picture can be painted. However, it is clear that there are three distinct phases: in the first phase (Baylei, Cymodoce and, in some measure, Mutabilis) the assemblages retain a characteristically Oxfordian allure: in the second, they have a distinct identity which may be termed characteristically Kimmeridgian: and in the third (Rotunda and Pallasioides) the assemblages begin to acquire Lower Cretaceous characters though still retaining a dominantly Upper Jurassic allure.

Thirty-eight species were observed to range throughout the Kimmeridgian: 26 further species were recorded both from the Lower and Upper and must be assumed to range through the Middle Kimmeridgian. Thirty seven species were recorded only from the Lower Kimmeridgian, seven others in the Lower and Middle Kimmeridgian. Five species occurred only in the Middle and Upper, four only in the Middle, nine only in the Upper Kimmeridgian. The imbalance in the number of characteristic species certainly reflects the imbalance in study. It is already possible to distinguish from the study of an assemblage, whether it is from the Lower, Middle or Upper Kimmeridgian: it should be possible, in the future, to determine that the sample came from a particular ammonite zone or from one of two adjacent zones.

Whether it will be possible in the future to distinguish, as well as to correlate between the assemblages from France, England and Scotland is less clear: the present authors consider that the similarities between the English and Scottish assemblages and those from northern France are so great as to make it virtually certain that these areas were all part of one plankton province in one water body (which agrees with what is known of Jurassic palaeogeography). Fuller information is needed on the assemblages from central France (Crussol and the Jura) before any meaningful commentary can be made, but it should be noted that surprisingly few of the species described from the latter locality by Deflandre (1939, 1941) were encountered in this study. Of 19 species described by Klement (1960) from the Kimmeridgian of South Germany, only seven were identified in the assemblages studied. It thus appears probable that these assemblages were drawn from a different plankton province, and hence a different water body. Future studies of these microfossils promise to aid in elucidating the pattern of water circulation in the Jurassic.

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PLATE 1

Tenua echinata sp. nov.

FIG. 1. General appearance and archaeopyle formation of the holotype, V.52796(1) ×716.

FIG. 9. Paratype, I.G.S. slide PK 119 ×450.

Chytroeisphaeridia chytroeides Sarjeant

FIG. 2. I.G.S. slide PK 102A ×1530.

Chytroeisphaeridia mantelli sp. nov.

FIG. 3. Holotype, showing archaeopyle with attached operculum. I.G.S. slide PK 116 ×560.

FIG. 4. Paratype A, I.G.S. slide PK 114 ×500.

Chytroeisphaeridia pococki Sarjeant

FIG. 5. BM(NH) slide V.53961(3) ×1600.

Fromea warlinghamensis sp. nov.

FIG. 6. Holotype (b) I.G.S. slide PK 115 ×720.

FIG. 8. Paratype BM(NH) slide V.56340 (1) ×510.

Tenua sp.

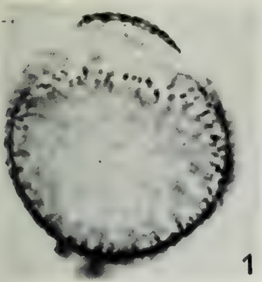
FIG. 7. BM(NH) slide V.53619 (1) ×690.

FIG. 10. Same specimen taken by phase contrast. ×690.

Tenua capitata (Cookson & Eisenack)

FIG. 11. Specimen with attached operculum. BM(NH) slide V.56341 ×840.

FIG. 12. Same specimen by phase contrast. ×840.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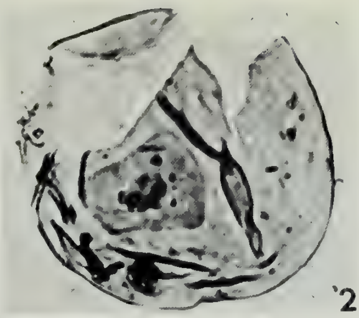
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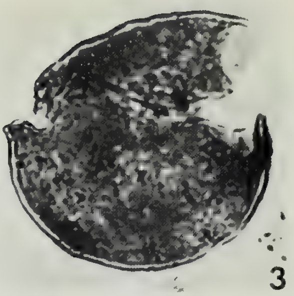
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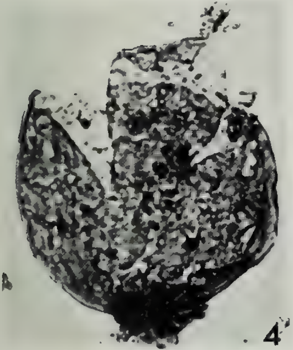
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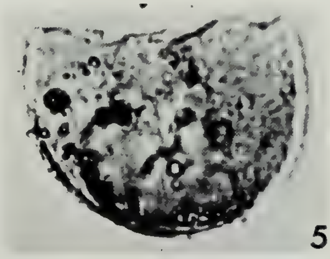
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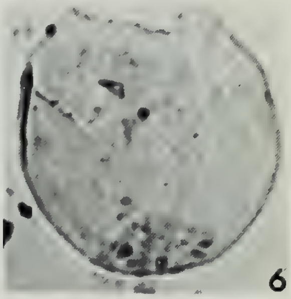
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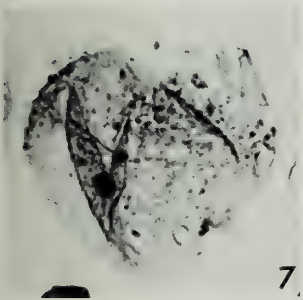
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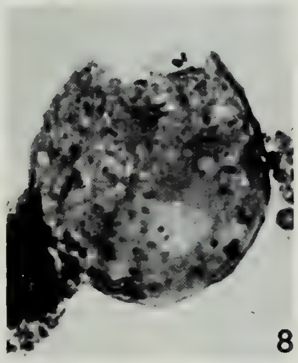
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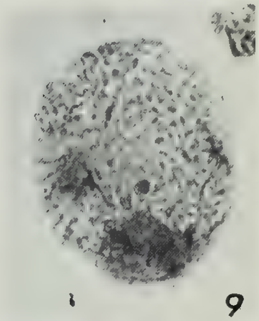
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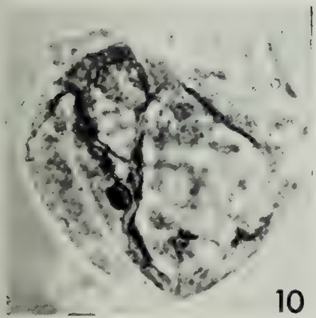
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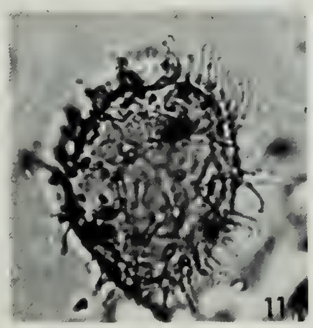
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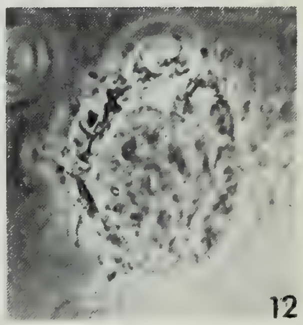
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PLATE 2

Gonyaulacysta cauda sp. nov.

Fig. 1. Ventral view of the holotype.
BM(NH) slide V.53965 (2) ×614.
Fig. 2. Dorsal view of the holotype. ×614.
Fig. 4. Ventral view of the paratype. BM(NH) slide V.56343 (1) ×716.
Fig. 5. Dorsal view of the paratype, by transparency. ×716.

Cryptarchaeodinium cf. ***calcaratum***

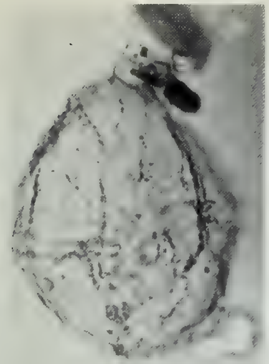
Fig. 3. Dorsal view. BM(NH) slide V.56342 ×c. 1,000.

Gonyaulacysta longicornis (Downie)

Fig. 6. A specimen from the Middle Kimmeridgian. I.G.S. slide PK 120. ×496.

Gonyaulacysta cladophora (Deflandre)

Fig. 7. I.G.S. slide PK 110. ×464. Sample WB7 (Eudoxus Zone).
Fig. 8. Same specimen by phase contrast. ×464.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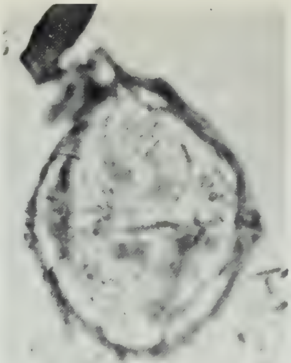
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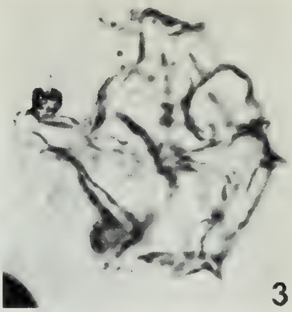
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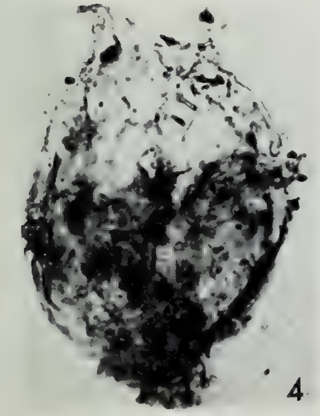
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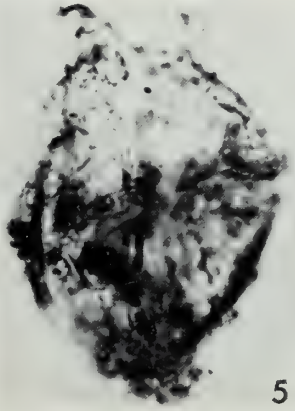
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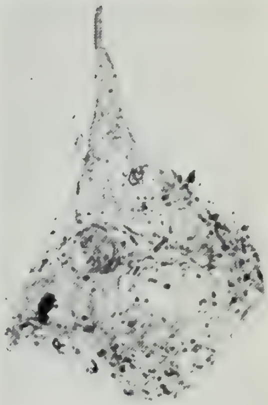
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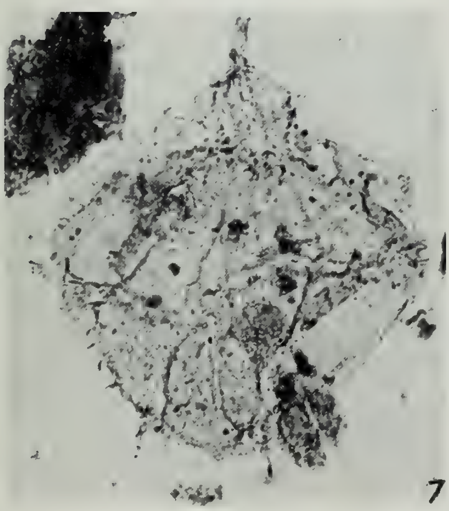
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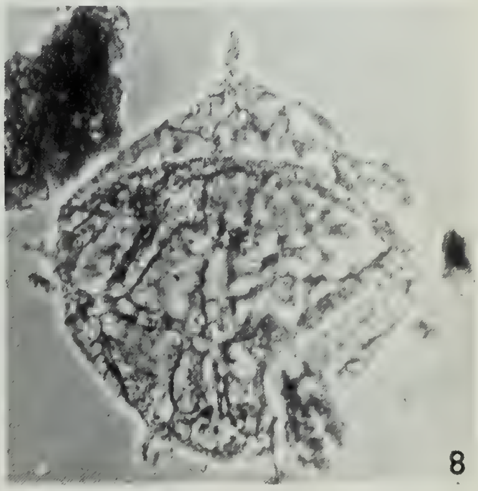
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PLATE 3

Gonyaulacysta globata sp. nov.

FIG. 1. Holotype, I.G.S. slide PK 122. ×625.

FIG. 2. Paratype BM(NH) slide V.56345. ×614.

Gonyaulacysta cf. **guiseppei** Morgenroth

FIG. 3. BM(NH) slide V.56344. Ventral view. ×600.

FIG. 4. Dorsal view of the same specimen, showing the archaeopyle. ×600.

Gonyaulacysta nuciformis (Deflandre)

FIG. 5. Ventral surface of specimen. I.G.S. slide PK 109. ×576.

Gonyaulacysta eisenacki (Deflandre)

FIG. 6. BM(NH) slide V.56375. Showing the ventral tabulation. ×890.

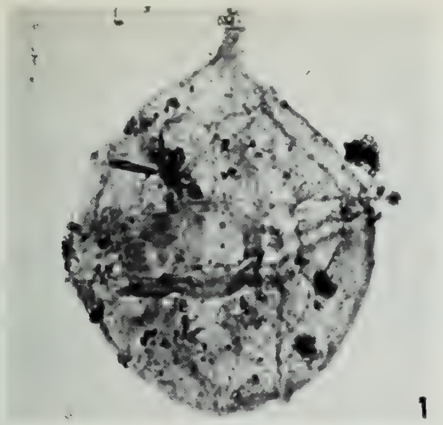
FIG. 7. Dorsal view of the same specimen. ×890.

Leptodinium cf. **crassinervum** (Deflandre)

FIG. 8. Specimen with detached operculum. BM(NH) slide V.56351 (1) ×384.

Leptodinium sp.

FIG. 9. BM(NH) slide V.56352. ×572.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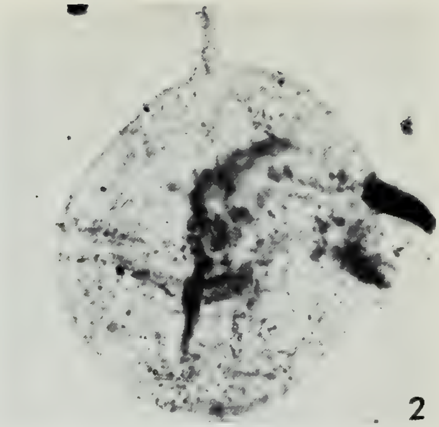
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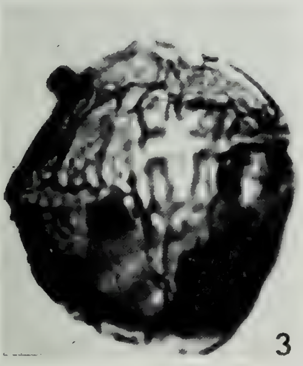
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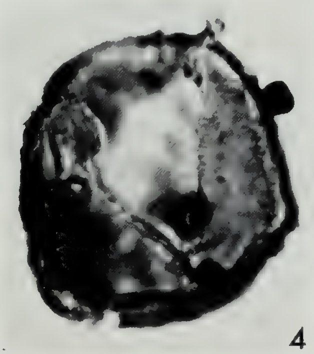
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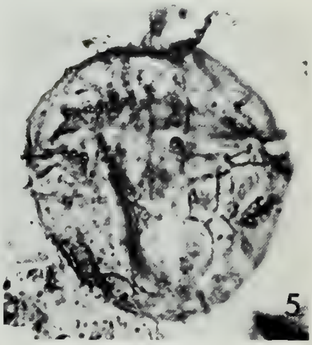
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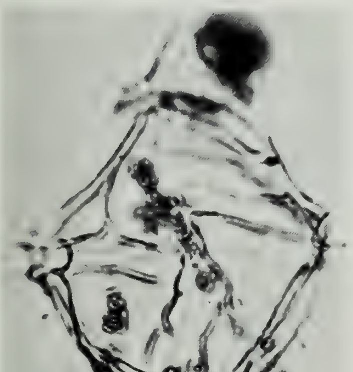
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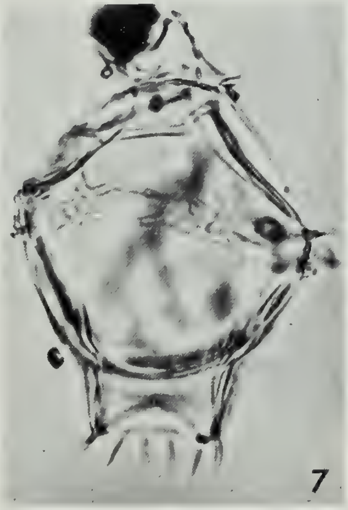
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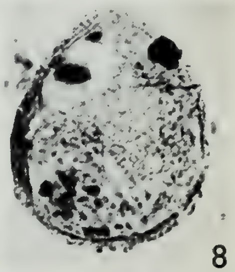
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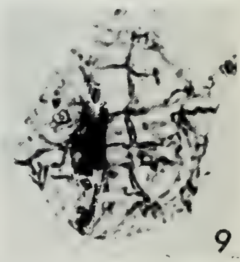
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PLATE 4

Gonyaulacysta longicornis (Downie)

FIG. 1. A specimen from the Upper Kimmeridgian. BM(NH) slide V.56346 (2). ×480.

Gonyaulacysta sp. B

FIG. 2. Ventral view of a specimen from the Middle Kimmeridgian. I.G.S. slide PK 117. ×840.

FIG. 3. Dorsal view of the same specimen. ×840.

Meiourogonyaulax sp.

FIG. 4. BM(NH) slide V.56359 (1). The operculum is still attached. ×614.

Meiourogonyaulax pila sp. nov.

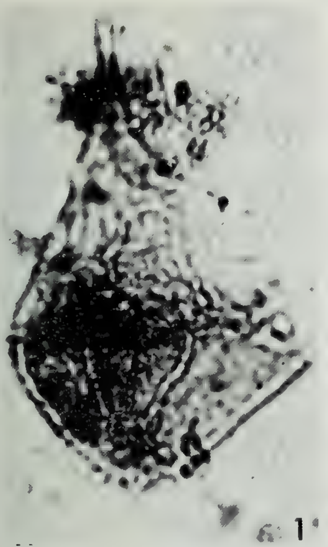
FIG. 5. BM(NH) slide V.56358. Holotype. ×691.

Gonyaulacysta perforans (Cookson & Eisenack)

FIG. 6. I.G.S. slide PK 131. ×1430.

Gonyaulacysta cf. ***mamillifera***

FIG. 7. I.G.S. slide PK 130. ×750.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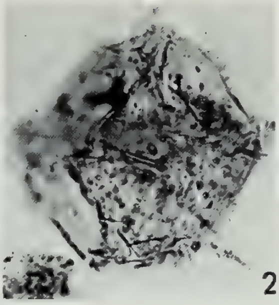
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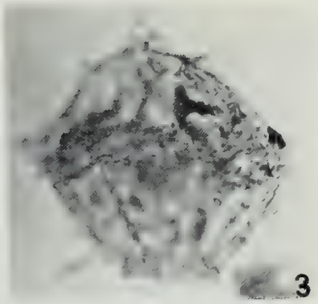
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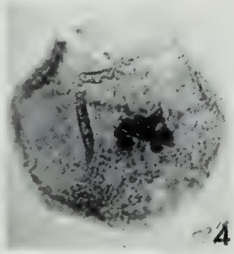
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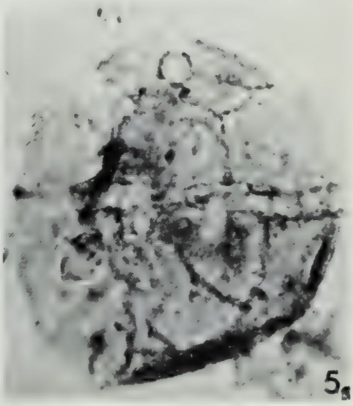
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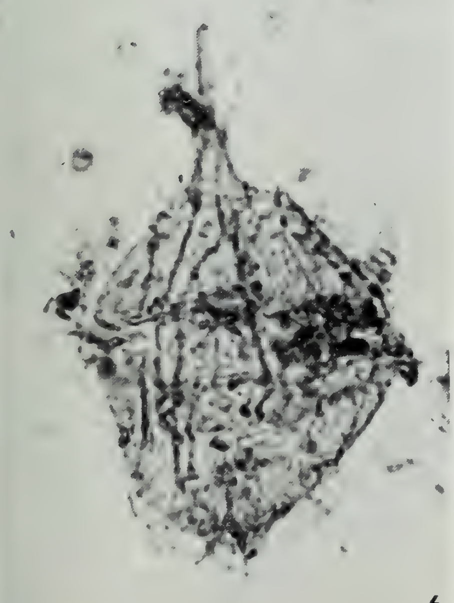
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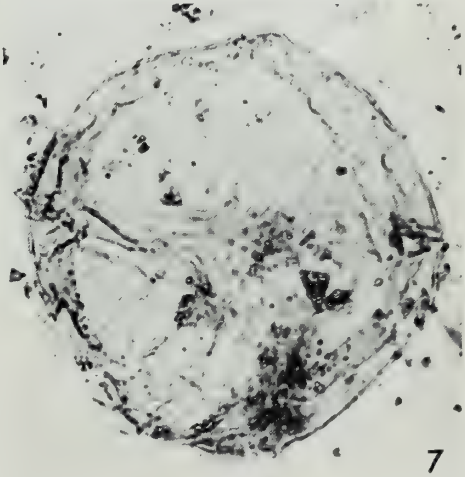
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PLATE 5

Leptodinium aceras (Eisenack)

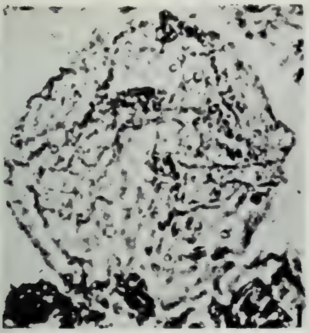
FIG. 1. Ventral surface. I.G.S. slide PK 108. ×640.
FIG. 2. Dorsal surface of the same specimen. ×640.
FIG. 3. A specimen from the Lower Kimmeridgian. I.G.S. slide PK 112. ×626.

Leptodinium cf. **crassinervum** (Deflandre)

FIG. 4. Tabulation on the ventral side. BM(NH) slide V.56346 (1 & 3). ×768.
FIG. 5. Dorsal surface of the same specimen; plate 3″ is lost in archaeopyle formation ×768.
FIG. 6. Dorsal view of another specimen, with operculum still attached. BM(NH) slide V.56351 (1). ×480.

Gonyaulacysta systremmatos sp. nov.

FIG. 7. Holotype BM(NH) slide V.53966 (1), showing the ventral surface. ×848.
FIG. 8. Dorsal view of the holotype. ×848.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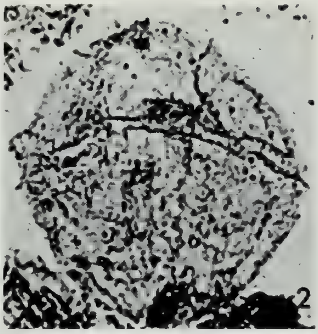
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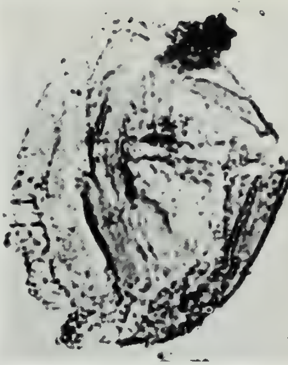
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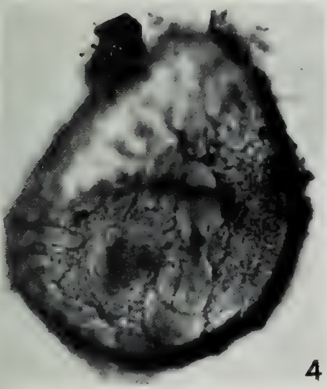
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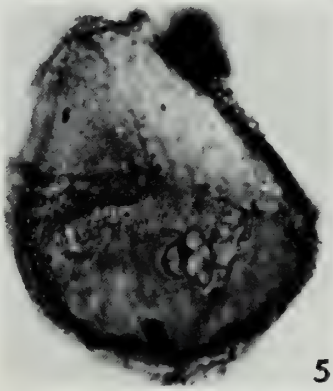
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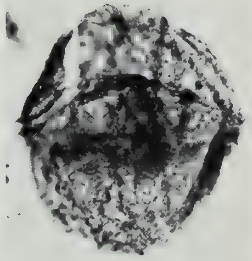
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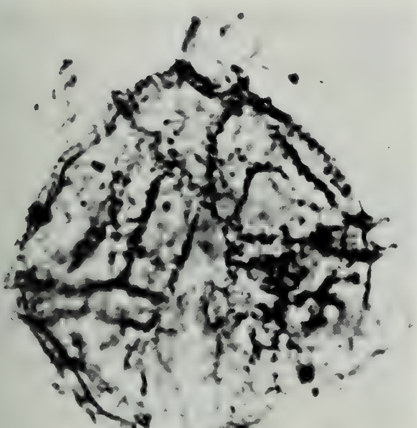
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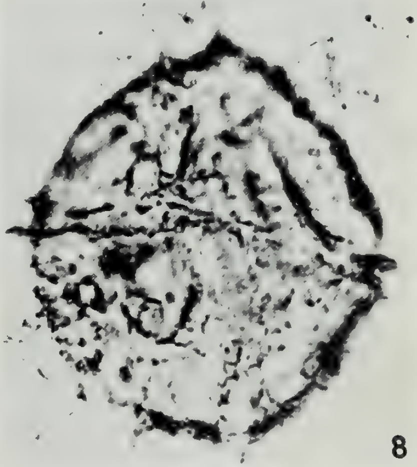
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PLATE 6

Gonyaulacysta **sp. C**

FIG. 1. I.G.S. slide PK 118. taken by phase contrast. ×656.
FIG. 2. Same specimen, by Nomarski interference contrast. ×656.

Gonyaulacysta **sp. F**

FIG. 3. Left lateral view. BM(NH) slide V.56348 (1). ×512.
FIG. 6. Right lateral view, as seen by Nomarski interference contrast. ×512.

Gonyaulacysta **sp. D**

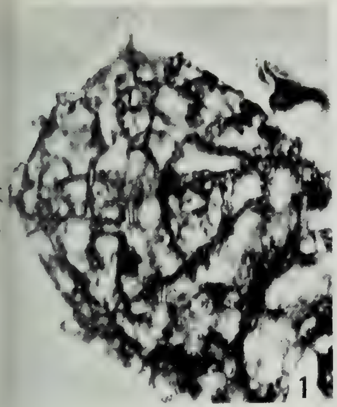
FIG. 4. Ventral view. BM(NH) slide V.56346 (4). ×580.
FIG. 5. Dorsal view of the same specimen. ×580.

Gonyaulacysta **sp. G**

FIG. 7. Ventral view. BM(NH) slide V.56349 (1). ×768.
FIG. 8. Dorsal view. ×768.

Gonyaulacysta **sp. E**

FIG. 9. Ventral view of the specimen. I.G.S. slide PK 113. ×680.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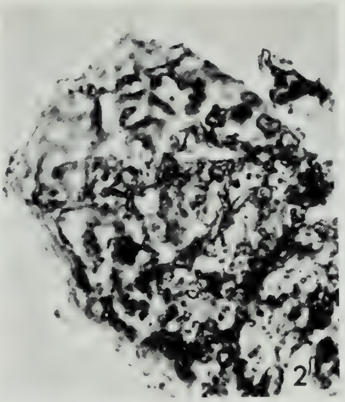
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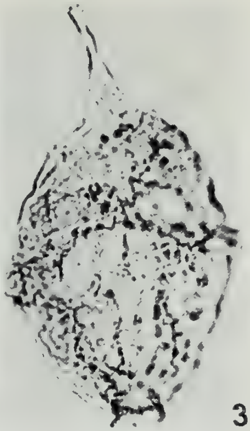
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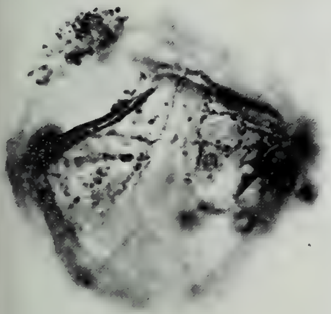
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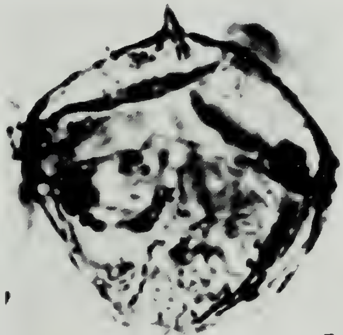
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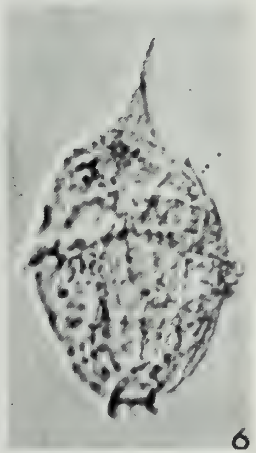
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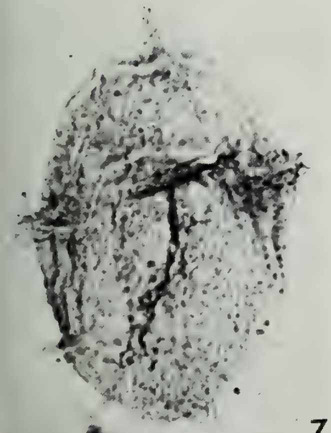
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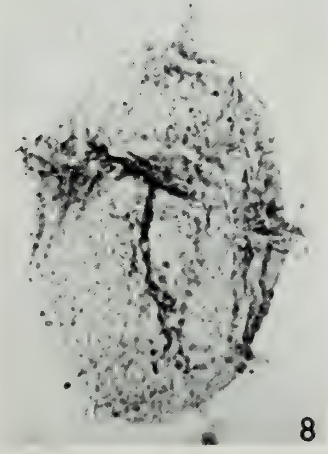
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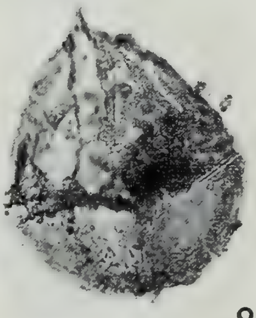
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PLATE 7

Leptodinium egemenii Gitmez

FIG. 1. Ventral surface of the paratype, BM(NH) slide V.52798 (3), by phase contrast. ×574.

FIG. 2. Dorsal view of the paratype: plate 3″ lost in archaeopyle formation. ×574.

Meiourogonyaulax pila sp. nov.

FIG. 3. General appearance of the paratype, showing the attached operculum. I.G.S. slide PK 121. ×544.

Dictyopyxis cf. **reticulata** (Valensi)

FIG. 4. Ventral surface of specimen. BM(NH) slide V.56354 (1). ×768.

FIG. 5. Dorsal view, showing the median band equivalent to a cingulum. ×768.

Meiourogonyaulax dicryptos sp. nov.

FIG. 6. Holotype, with apical archaeopyle; taken using Nomarski interference contrast. BM(NH) slide V.56357 (1). ×704.

Histiophora cf. **ornata**

FIG. 7. Specimen with apical archaeopyle. BM(NH) slide V.52964 (1). ×768.

FIG. 8. Same specimen, taken by phase contrast. ×768.

Dictyopyxis areolata Cookson & Eisenack

FIG. 9. BM(NH) slide V.53956 (1). Specimen with apical archaeopyle. ×614.

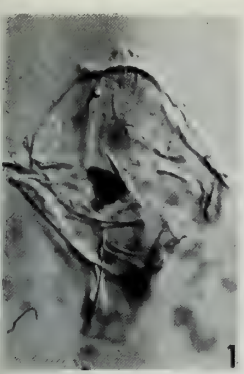
Occisucysta monoheuriskos sp. nov.

FIG. 10. Ventral view of the holotype. BM(NH) slide V.56353 (1). ×615.

FIG. 11. Dorsal view of the holotype, showing the two-plate precingular archaeopyle. ×615.

Meiourogonyaulax sp.

FIG. 12. Specimen with attached operculum. I.G.S. slide PK 100. ×1200.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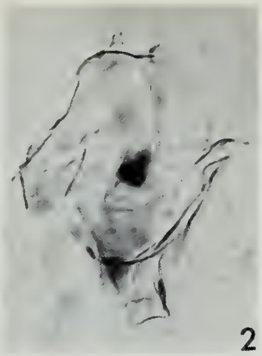
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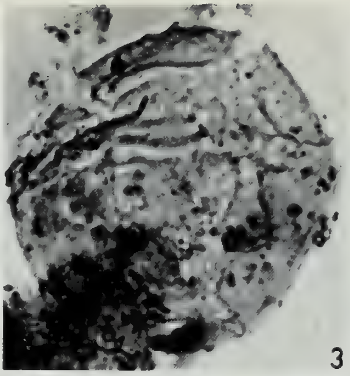
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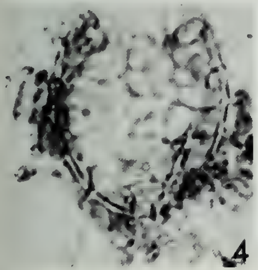
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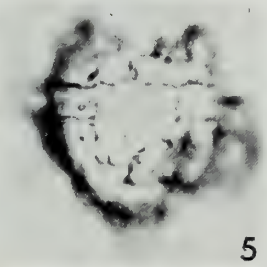
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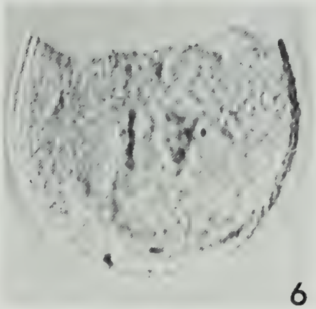
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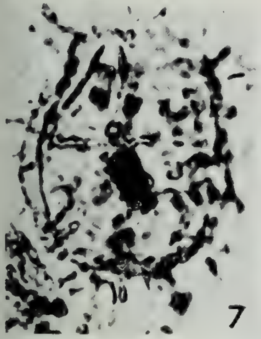
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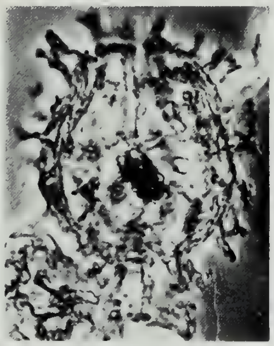

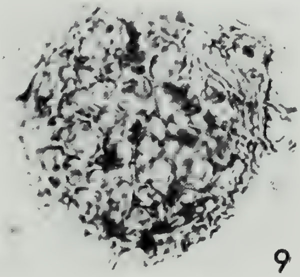
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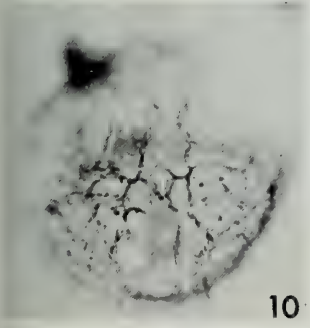
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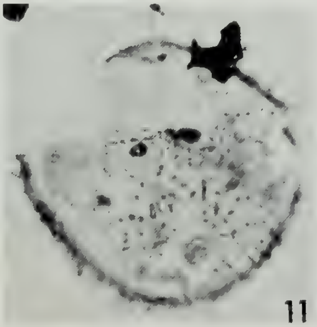
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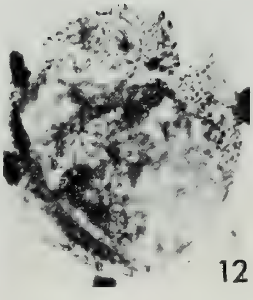
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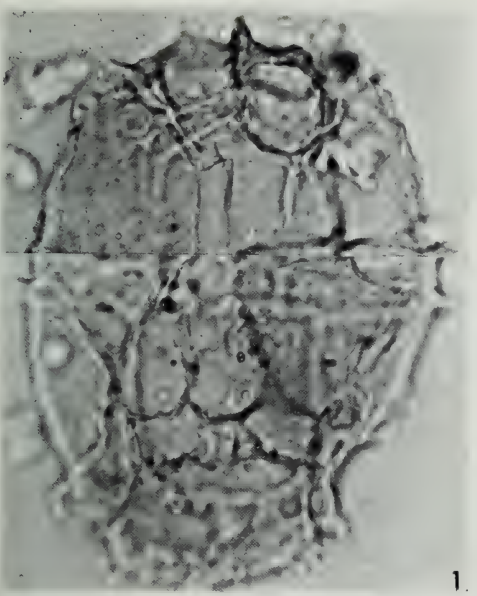
PLATE 8

Egmontodinum polyplacophorum gen. et. sp. nov.

FIGS. 1–2. Holotype, BM(NH) slide V.56360 (2b). 1. In ventral view. 2. In dorsal view, by transparency. ×1215.

FIGS. 3–4. Paratype (a), BM(NH) slide V.56360. 3. In oblique ventral view, by transparency details of posterior not visible. 4. In oblique dorsal view. ×1215.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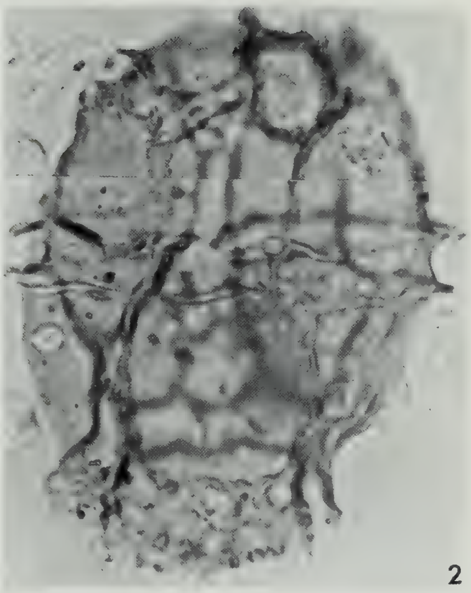
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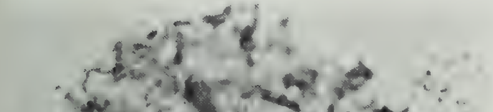
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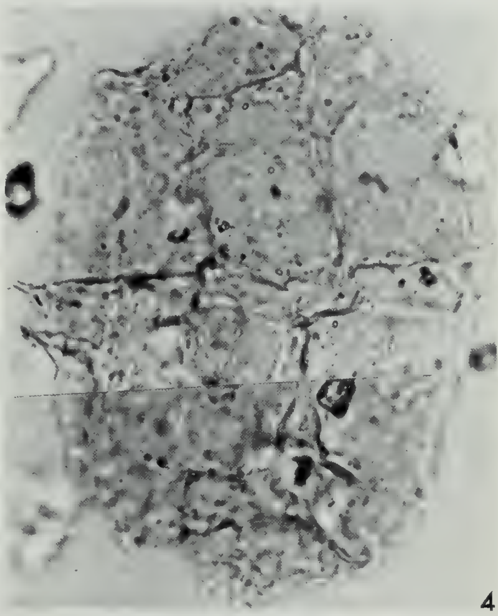
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PLATE 9

Gonyaulacysta sp. A Gitmez and herein

FIG. 1. BM(NH) slide V.56347 (2). ×720.

FIG. 2. Detail of apex by phase contrast, showing the short spines on crests. ×1215.

Egmontodinium polyplacophorum gen. et. sp. nov.

FIG. 3. Paratype (c), showing apical archaeopyle. BM(NH) slide V.56347 (1). ×720.

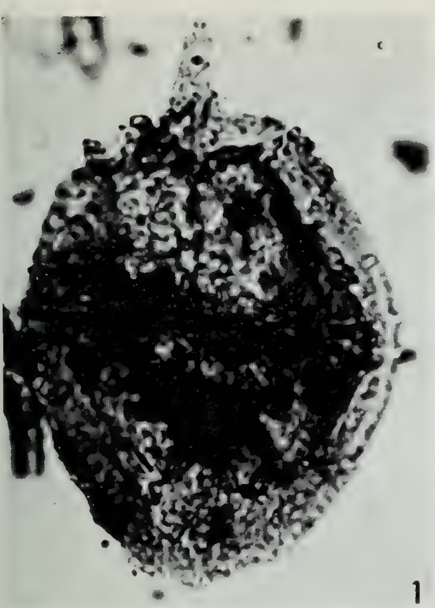
Meiourogonyaulax staffinensis Gitmez

FIG. 4. BM(NH) slide V.56356. ×c. 720.

Fromea warlinghamensis sp. nov.

FIG. 5. Paratype (a), BM(NH) slide V.56339 (2). ×720.

FIG. 6. Detail of surface, showing bulges and polygonal patterning considered to be produced by pressure of mineral grains. ×215.



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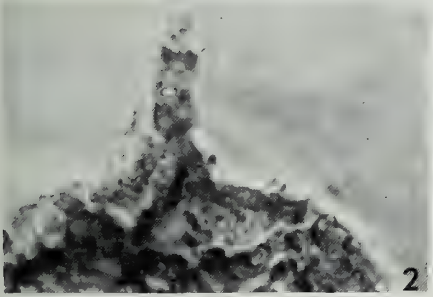

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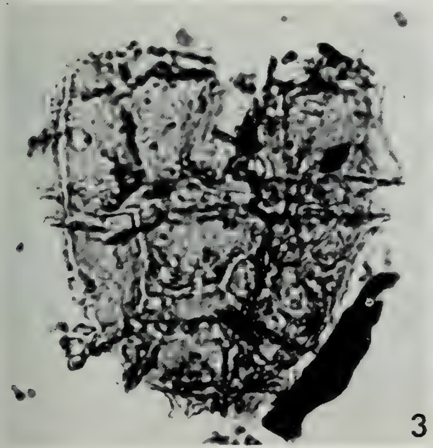

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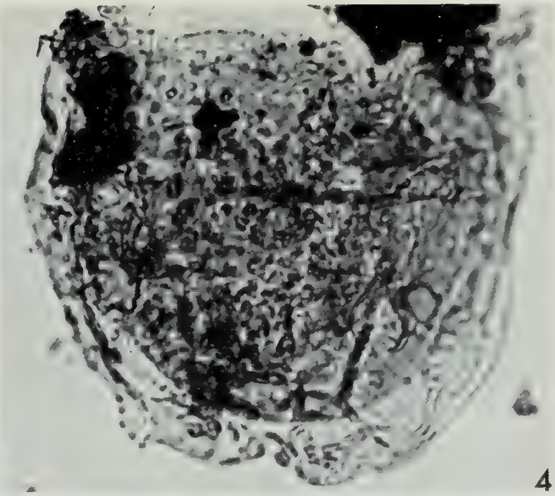

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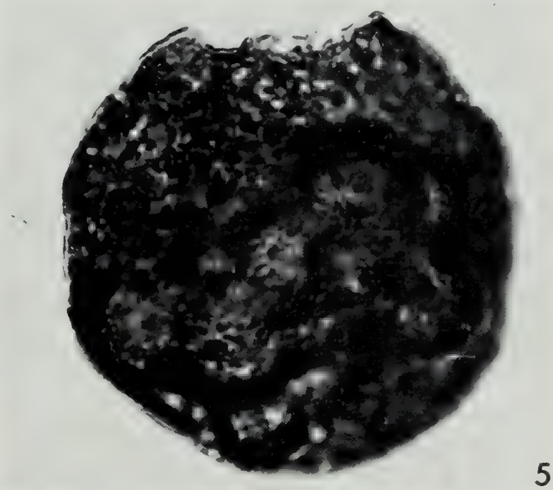

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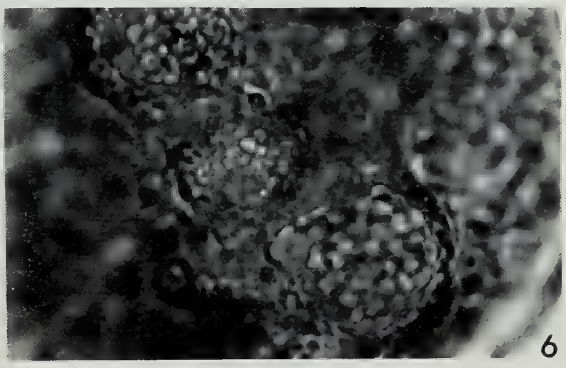

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PLATE 10

Adnatosphaeridium paucispinum (Klement)

FIG. 1. BM(NH) slide V.56365 (1). ×480.

FIG. 2. Same specimen taken by phase contrast. ×480.

FIG. 3. Specimen with apical archaeopyle. BM(NH) slide V.56366 (2). Ventral view, by phase contrast. ×544.

FIG. 4. Dorsal view of the same specimen by phase contrast. ×544.

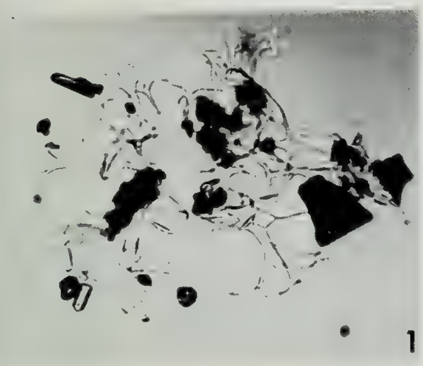
Leptodinium amabilis (Deflandre)

FIG. 5. Ventral view. BM(NH) slide V.56350 (1). ×1200.

FIG. 6. Dorsal view of the same specimen, showing the precingular archaeopyle. ×1200.

Cleistosphaeridium ehrenbergi (Deflandre)

FIG. 7. BM(NH) slide V.56376 Sample LO353, by phase contrast. ×651.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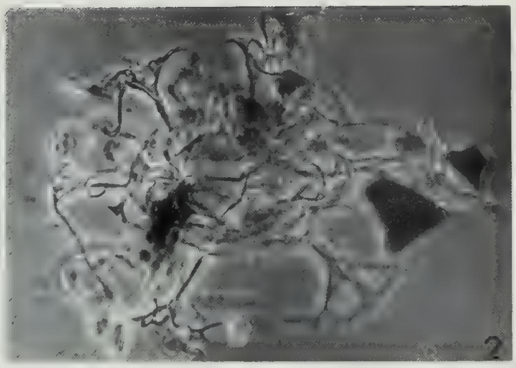
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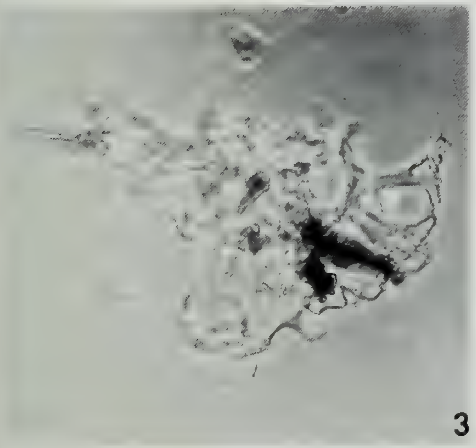
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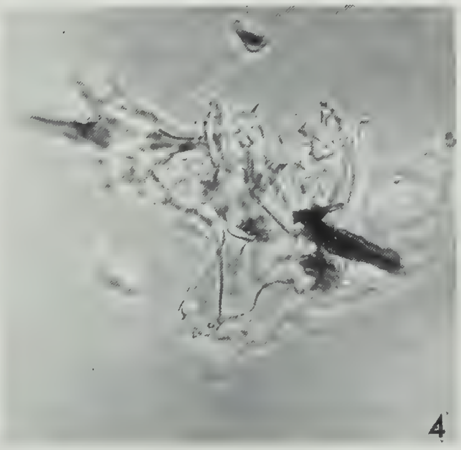
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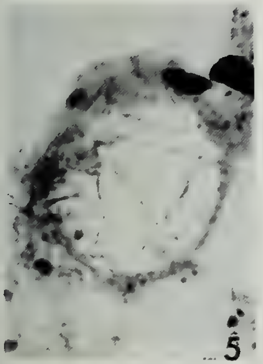
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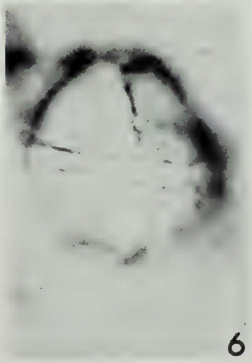
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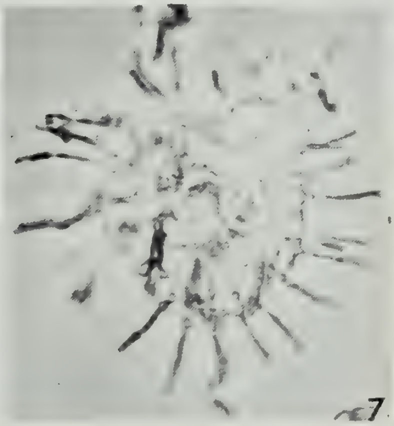
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PLATE 11

Imbatodinium cf. **villosum** Vozzhennikova

FIG. 1. BM(NH) slide V.56362 (1); specimen from the Upper Kimmeridgian of Dorset. ×608.

Imbatodinium antennatum sp. nov.

FIG. 2. Paratype, showing the intercalary archaeopyle. BM(NH) slide V.56361 (1). ×768.

FIG. 3. Holotype, showing the intercalary archaeopyle. I.G.S. slide PK 124. ×845.

Proximate cyst sp. indet.

FIG. 4. Specimen with attached operculum. BM(NH) slide V.56363 (1). ×513.

FIG. 7. Same specimen, taken by Nomarski interference contrast. ×513.

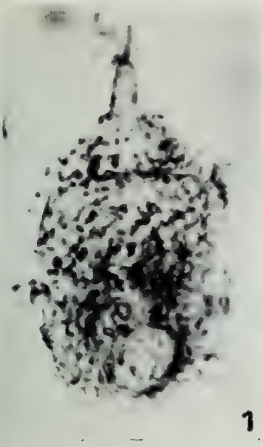
FIG. 9. General view of another specimen; BM(NH) slide V.56364. ×451.

Egmontodinium polyplacophorum gen. et. sp. nov.

FIG. 5. Holotype in ventral view, showing the tabulation. BM(NH) slide V.56360 (2b). ×640.

FIG. 6. Dorsal view of the holotype, by transparency. ×640.

FIG. 8. Paratype (c), showing apical archaeopyle. BM(NH) slide V.56347 (1). ×1024.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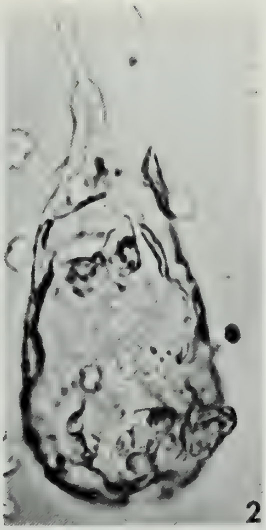
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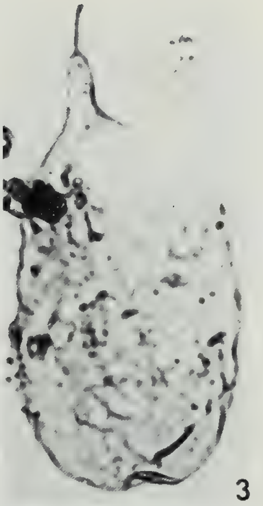
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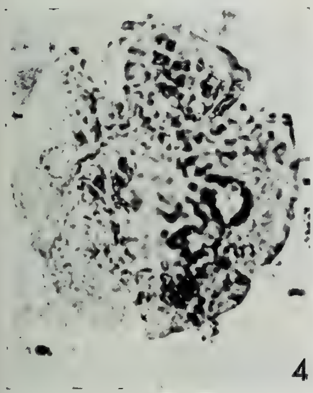
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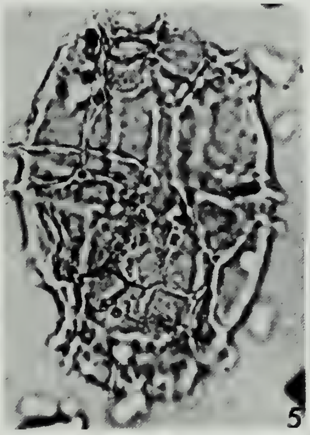
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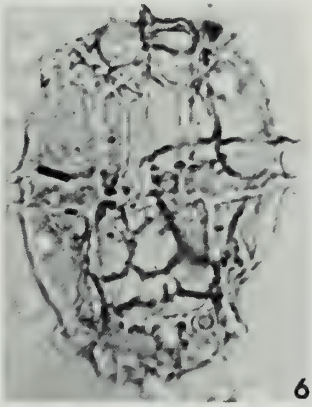
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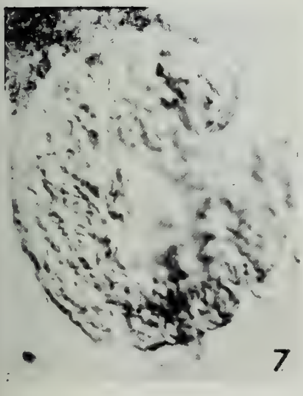
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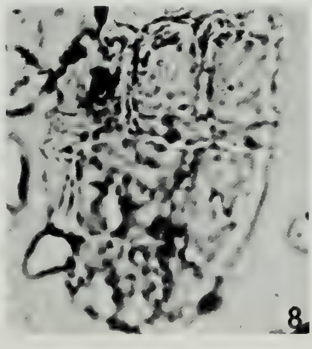
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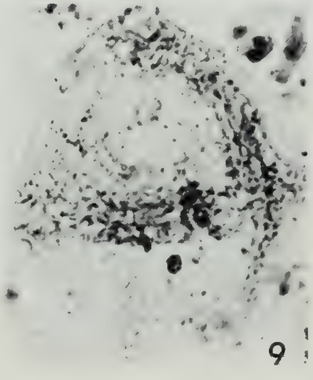
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PLATE 12

Dictyopyxis cf. **reticulata** (Valensi)

FIG. 1. In presumed oblique ventral aspect. BM(NH) slide V.56355 (1). ×768.

FIG. 2. Same specimen in presumed oblique dorsal aspect showing the apical archaeopyle. ×768.

Chytroeisphaeridia mantelli sp. nov.

FIG. 3. Paratype B, showing the archaeopyle and slits. BM(NH) slide V.56338 (1). ×532.

Apteodinium granulatum Eisenack

FIG. 4. Ventral view of specimen. I.G.S. slide PK102. ×592.

FIG. 5. Dorsal view of the same specimen, showing the precingular archaeopyle. ×592.

Apteodinium cf. **maculatum** Eisenack & Cookson

FIG. 6. I.G.S. slide PK 105. ×464.

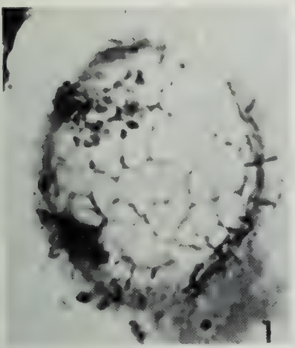
Pterospermopsis australiensis Deflandre & Cookson

FIG. 7. BM(NH) slide V.56353 (2) Sample CS421. ×1000.

Polystephanephorus sarjeantii Gitmez

FIG. 8. Holotype by phase contrast. BM(NH) slide V.52792 (2), sample OM 131. ×580.

FIG. 9. Holotype showing the apical archaeopyle. (Phase contrast). ×580.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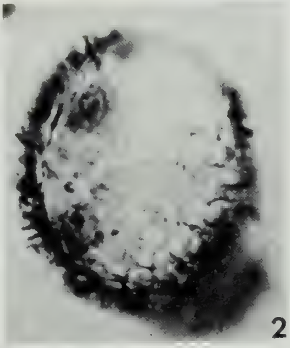
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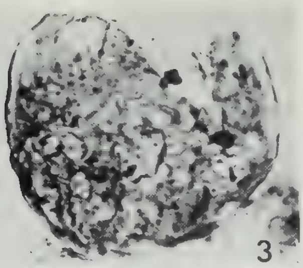
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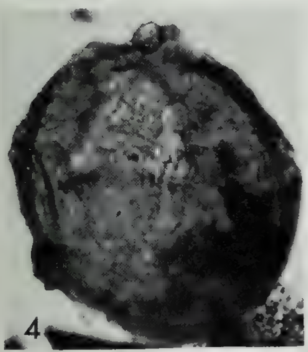
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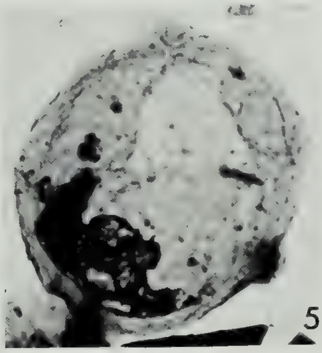
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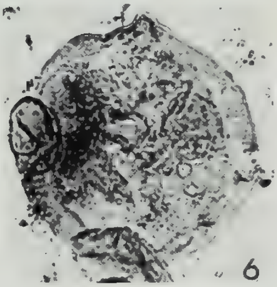
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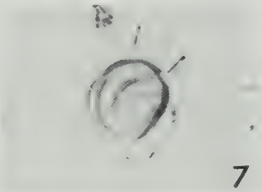
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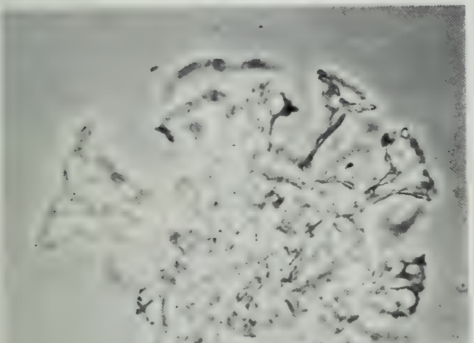
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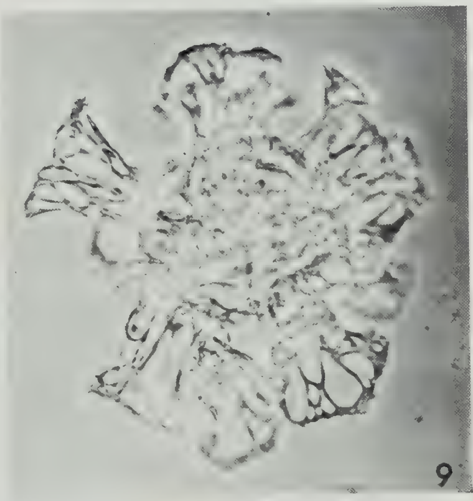
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PLATE 13

Gonyaulacysta sp. H

FIG. 1. Oblique ventral view BM(NH) slide V.56339 (1), sample CH231. ×720.

Systematophora orbifera Klement

FIG. 2. Showing apical archaeopyle. BM(NH) slide V.56377, sample OM 418. ×720.

Oligosphaeridium pulcherrimum (Deflandre & Cookson)

FIG. 3. BM(NH) slide V.56368 (1), sample CC 449. ×800.

Scriniodinium sp.

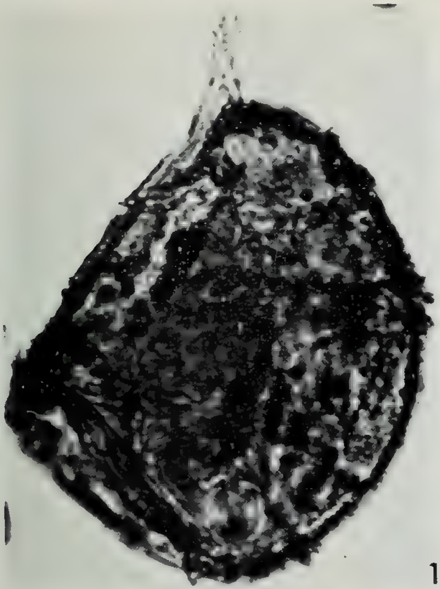
FIG. 4. Ventral view of the specimen I.G.S. slide PK 107. ×448.

Prolixosphaeridium granulosum (Deflandre)

FIG. 5. BM(NH) slide V.52799 (4); from the sample OM 131. ×768.

FIG. 6. Specimen with attached operculum. I.G.S. slide PK 103. ×573.

FIG. 7. Specimen lacking the operculum. BM(NH) slide V.53960 (3). Sample SC 444. ×1024.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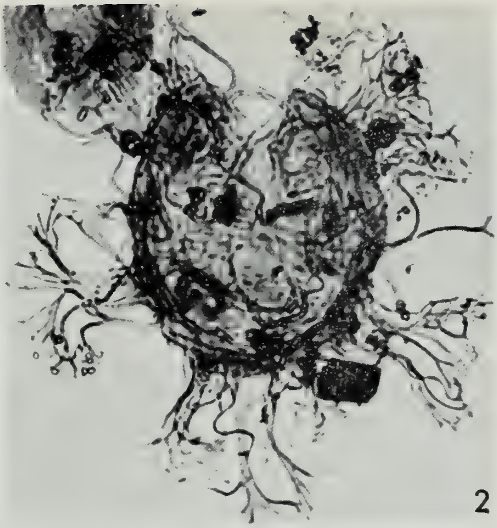
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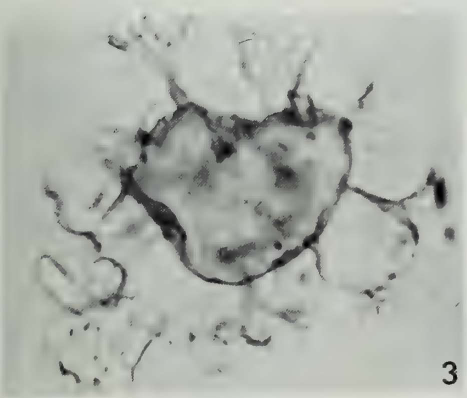
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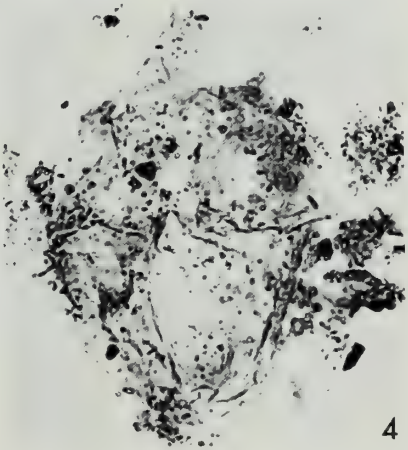
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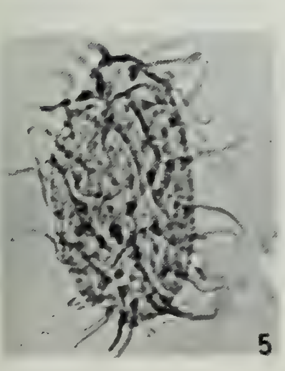
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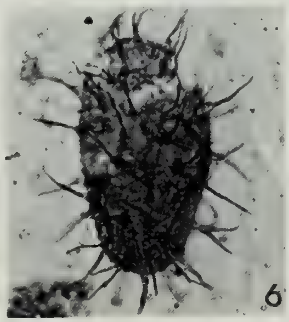
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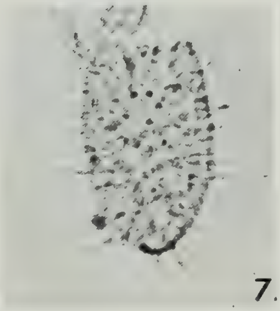
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PLATE 14

Systematophora ovata sp. nov.

FIG. 1. Paratype. BM(NH) slide V. 56343 (2) ×717.

FIG. 2. Holotype, with apical archaeopyle. BM(NH) slide V.53962 (1). ×800.

FIG. 3. Same specimen, under phase contrast. ×800.

Parvocavatus tuberosus Gitmez

FIG. 4. BM(NH) slide V.56353 (3). Sample ES 421. ×1075.

Hexagonifera jurassica sp. nov.

FIG. 5. Holotype, with attached operculum. I.G.S. slide PK 123. ×350.

FIG. 8. Paratype with apical archaeopyle. BM(NH) slide V.53621 (1). ×819.

Stephanelytron redcliffense Sarjeant

FIG. 6. BM(NH) slide V.56366 (1). ×840.

Stephanelytron cf. ***redcliffense*** Sarjeant

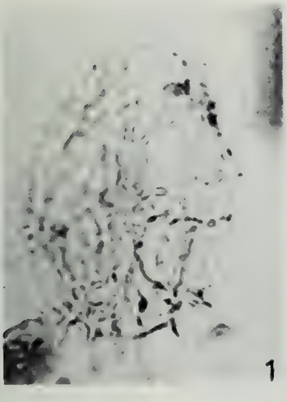
FIG. 7. Specimen with apical archaeopyle. BM(NH) slide V.56365 (2). ×768.

Endoscrinium sp.

FIG. 9. Ventral view of the specimen by phase contrast. BM(NH) slide V.56369 (1). ×640.

FIG. 10. Ventral view of same specimen, by ordinary light. ×480.

FIG. 11. Dorsal view of same specimen showing the precingular archaeopyle. ×480.



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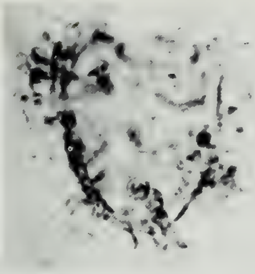

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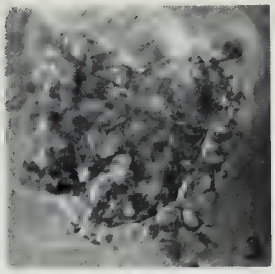

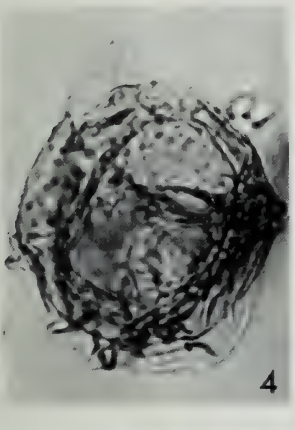

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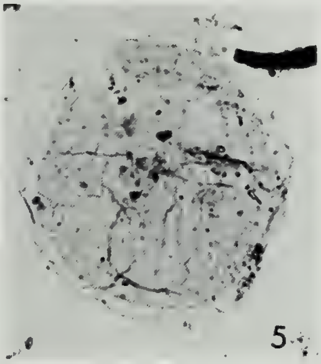

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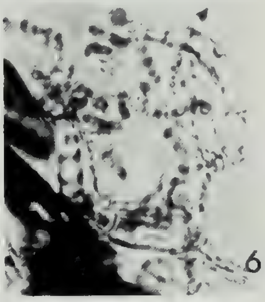

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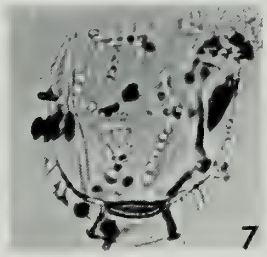

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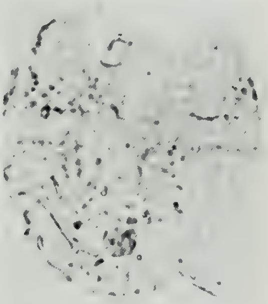

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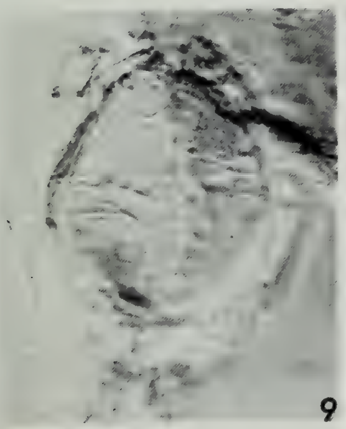

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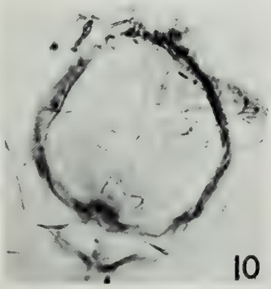

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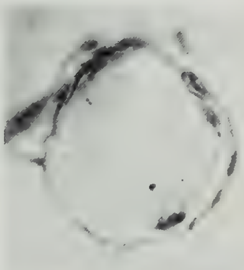

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PLATE 15

Muderongia simplex Alberti

FIG. 1. I.G.S. slide PK 128. ×720.

FIG. 2. Specimen showing the apical archaeopyle. I.G.S. slide PK 129. ×922.

Cleistosphaeridium sp.

FIG. 3. BM(NH) slide V.56367 (1). ×720.

Scriniodinium bicuneatum (Deflandre)

FIG. 4. BM(NH) slide V.56370. ×752.

Scriniodinium dictyotum subsp. **osmingtonensis** Gitmez

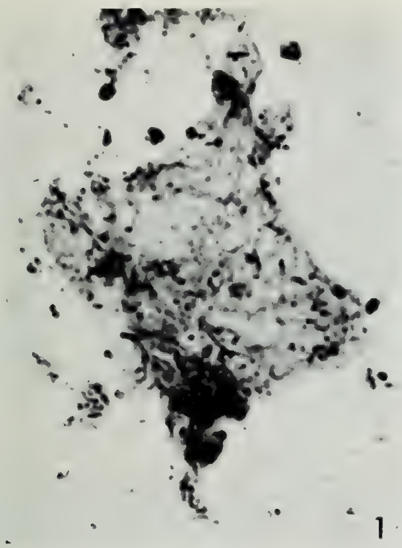
FIG. 5. BM(NH) slide V.52799 (1) sample OM 131. Holotype, without prominence at the apex. ×471.

Scriniodinium dictyotum subsp. **papillatum** Gitmez

FIG. 6. Holotype, with precingular archaeopyle, showing the blunt, mammelon-shaped apical prominence. BM(NH) slide V.53940 (1). ×480.

Scriniodinium dictyotum subsp. **pyrum** Gitmez

FIG. 7. Specimen with strong apical horn. BM(NH) slide V.56371.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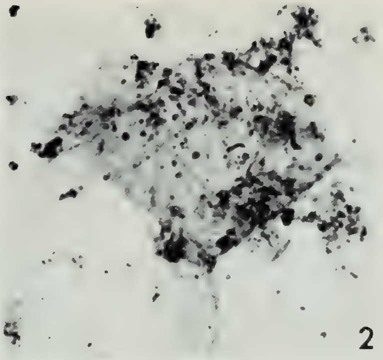
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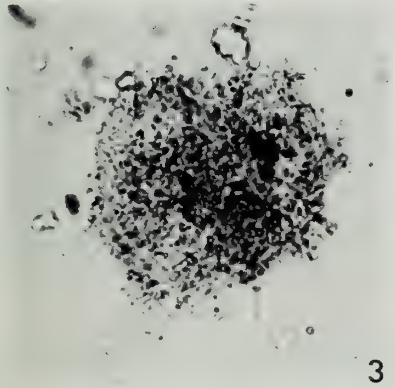
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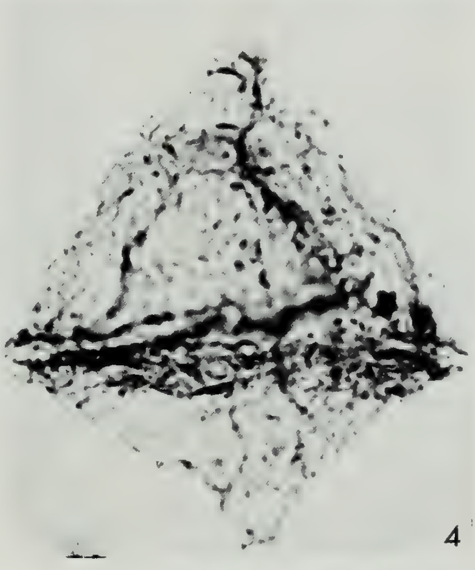
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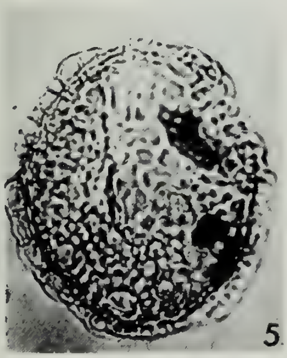
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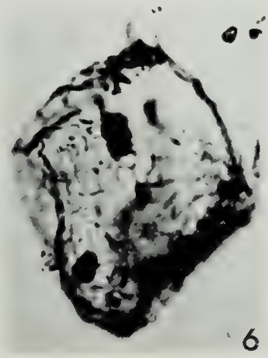
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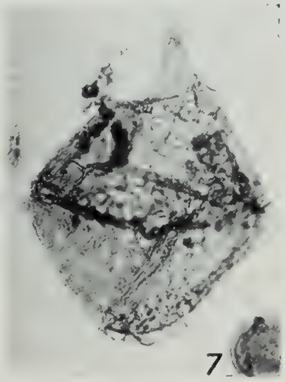
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PLATE 16

Organism A

FIG. 1. BM(NH) slide V.53948 (3). General appearance. ×691.

Cavate cyst sp. indet. B

FIG. 2. I.G.S. slide PK 104. ×640.

FIG. 4. I.G.S. slide PK 106. ×640.

Cavate cyst sp. indet. A

FIG. 3. I.G.S. slide PK 102C (3). ×640.

Pterospermopsis helios Sarjeant

FIG. 5. BM(NH) slide V.53963 (1). Sample SC 144 (Baylei Zone). ×2100.

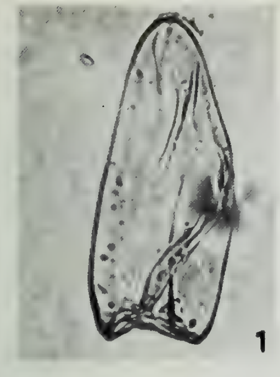
Scriniodinium dictyotum subsp. ***dictyotum*** Cookson & Eisenack

FIG. 6. Specimen with a slight apical prominence. BM(NH) slide V.56372 (1). ×496.

Sirmiodinium grossi Alberti

FIG. 7. Dorsal view of specimen. BM(NH) slide V.56373 (1). ×896.

FIG. 8. Specimen with apical archaeopyle. BM(NH) slide V.56374 (1). ×941.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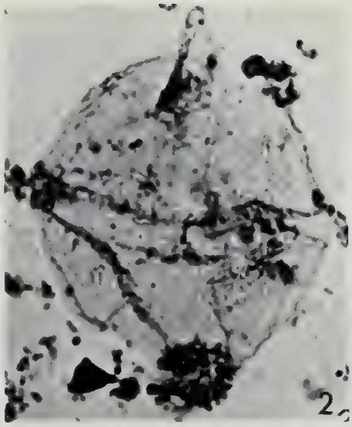
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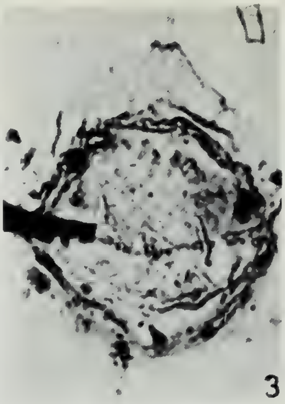
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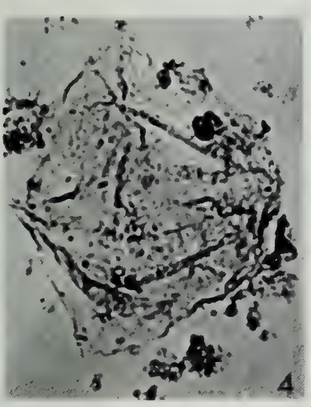
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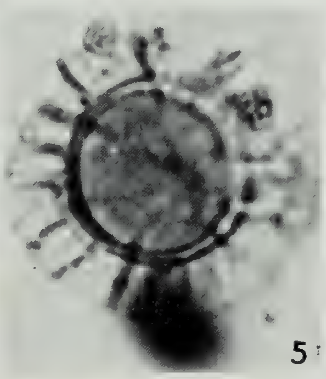
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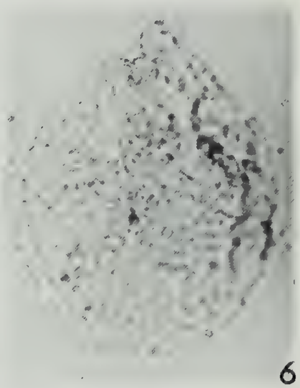
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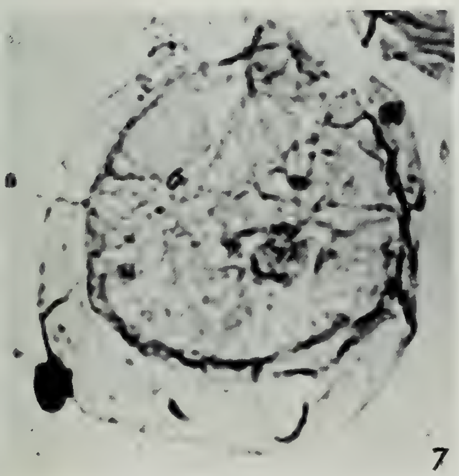
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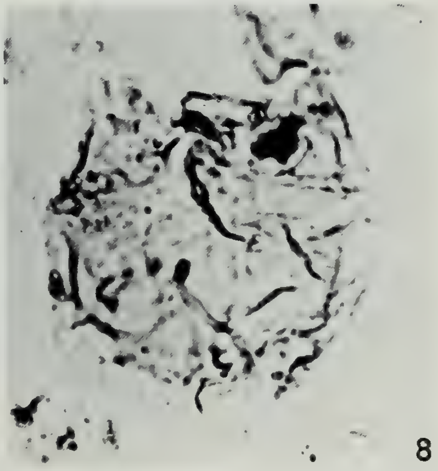
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PLATE 17

Micrhystridium recurvatum Valensi

Fig. 1. I.G.S. slide PK 127. ×1276.
Fig. 2. The other side of the same specimen. ×1276.

Organism A

Fig. 3. BM(NH) slide V.53948 (3). Phase contrast objective used. ×768.

Acritarch sp. indet.

Fig. 4. Specimen with opening. I.G.S. slide PK 125. × 1200.
Fig. 5. Another specimen with opening. I.G.S. slide PK 126. × 1400.

Pterospermopsis harti Sarjeant

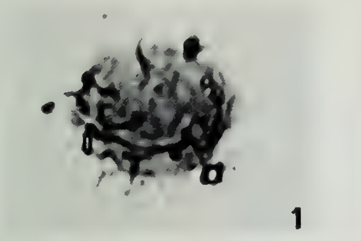
Fig. 6. I.G.S. slide PK 111. ×1085.

Micrhystridium sp.

Fig. 7. BM(NH) slide V.53953 (1). ×1280.
Fig. 8. Phase contrast view of same specimen. ×1280.

Solisphaeridium claviculorum (Deflandre)

Fig. 9. I.G.S. slide PK 101. ×1320.
Fig. 10. Phase contrast view of specimen. ×1320.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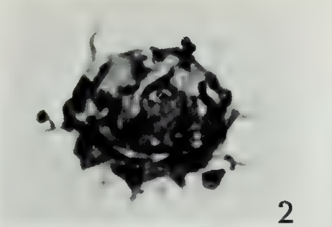
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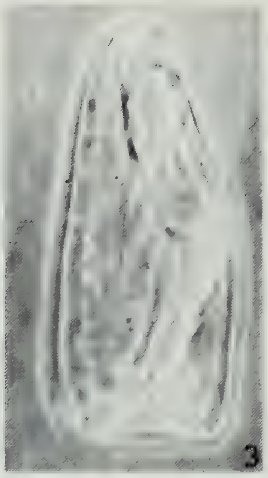
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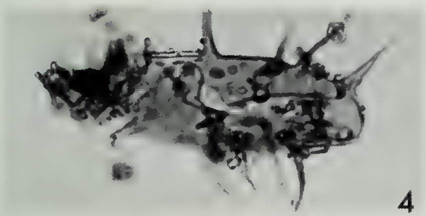
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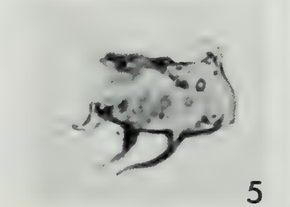
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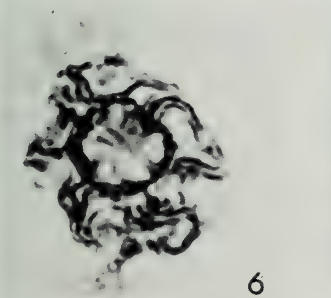
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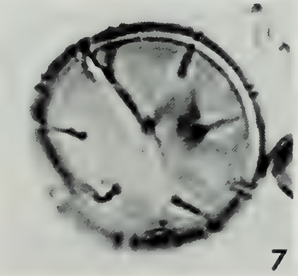
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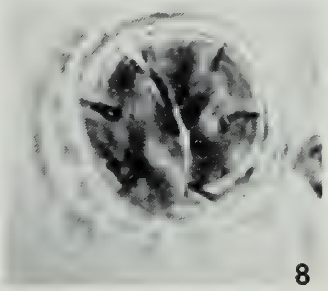
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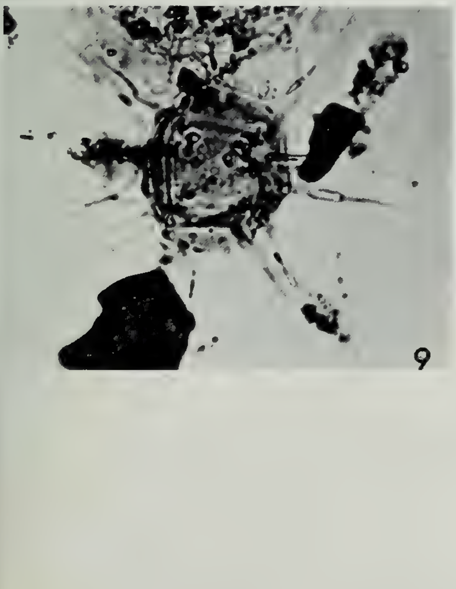
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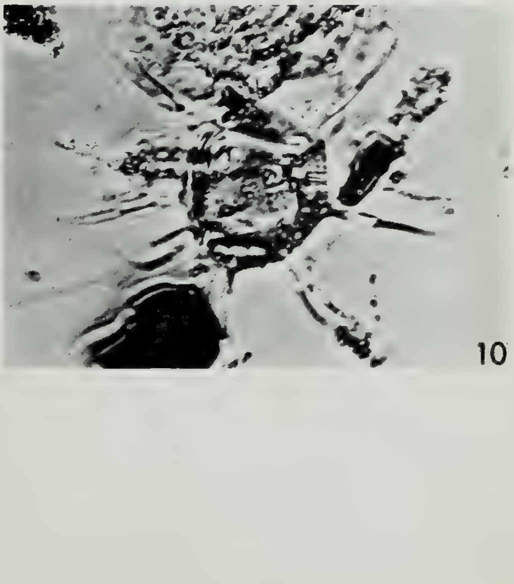
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MID-TERTIARY CYTHERETTINAE OF NORTH-WEST EUROPE

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NATURAL HISTORY

M. C. KEEN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 21 No. 6
LONDON : 1972

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BY

MICHAEL CHARLES KEEN
Glasgow University

Pp. 259–349; 23 *Plates*, 30 *Text-figures*

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LONDON: 1972

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By M. C. KEEN

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SUMMARY

Fifty eight species and subspecies of *Cytheretta* and ten of *Flexus* are described from the Middle and Upper Eocene and the Oligocene of western Europe. New species and subspecies are: from the Bartonian of the Paris Basin, *Cytheretta costellata grandipora, C. costellata cratis, C. carita, C. cellulosa, C. ruelensis,* and *Flexus ludensis*; from the Upper Eocene of the Hampshire

Basin, *C. costellata antecalva*, *C. forticosta*, *C. porosacosta*, *F. solentensis solentensis* and *F. solentensis congestus*; from the Oligocene of the Paris Basin, *C. tenuipunctata absoluta*, *C. tenuipunctata lirata*, *C. tenuistriata ornata*, *C. minipunctata*, *C. buttensis buttensis*, *C. buttensis reticulata*, *C. posticalis parisiensis*, *C. vesca*, and *C stigmosa gallica*; and from the Oligocene of the Aquitaine Basin, *C. oligocaenica*, *C. regularis*, *C. bullans*, *C. gibberis*, *C. sagri inconstans*, *C. sagri martini*, *C. minipustulosa*, *C. postornata*, and *F. lenijugum*. The stratigraphical distribution, ecology, and classification are also discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The following study of the subfamily Cytherettinae is mainly concerned with Upper Eocene and Oligocene species, but also includes some from the Lutetian, from possible Miocene, and from the Pliocene and Recent. The area covered includes the Hampshire Basin, the Paris Basin, Belgium and the Aquitaine Basin.

The study is taken from a Ph.D. thesis completed at the University of Leicester in 1967. Since then the Geology Department has had a scanning electron microscope installed, and through the permission of Prof. P. C. Sylvester-Bradley it has been possible to re-photograph the ostracods. This has sometimes brought out characters which are not very clear under an optical microscope, and very high magnifications are possible which show features not visible at all with an ordinary microscope. The photographs were taken by Mr G. Mc. Turk, to whom thanks are extended.

The stratigraphy of the Upper Eocene and Oligocene in Western Europe is complicated but the nomenclature of the stage names is even more so. There are some thirteen of the latter in common usage between the Lutetian and the Chattian, so to avoid confusion formation names are used where possible. When stage names are used however, they refer to the current usage in the particular area under discussion. When two or more areas are mentioned, the classification adopted is that of Wrigley & Davis (1937). Recent reviews of the stratigraphy can be seen in Batjes (1959), Cavelier (1964, 1965), Curry (1965, 1966), and Vigneaux (1964).

There are three main problems for the correlation of the mid-Tertiary within western Europe. The first is the relationship between the Middle and Upper Eocene; the second is the difficulty of recognizing the Bartonian in Belgium and the Paris Basin; and finally the placing of the Eocene-Oligocene boundary. Recent symposia at Bordeaux (1962), Paris (1968), and Marburg (1969) have failed to adopt any firm conclusions on any of these points. Most of the traditional concepts are under debate, and with so many ideas in the air correlation charts become redundant very quickly. Fig. 1 lists the horizons sampled for *Cytheretta* and also gives a tentative correlation.

The species concept adhered to in this work is narrower than has perhaps been usual with Tertiary ostracods. The reasons for this are, first, that by studying one subfamily it is possible to follow its geographical and stratigraphical ramifications. Secondly, comparisons have been made with type material whenever possible. Finally, it is my belief that it is only through the detailed studies of small groups of ostracods that they will take their rightful place for use in Tertiary stratigraphical correlation.

	PARIS BASIN	BELGIUM	HAMPSHIRE BASIN	RHINE / GERMANY	AQUITAINE BASIN	
					North	South
OLIGOCENE	FALUNS D'ORMOY MORIGNY JEURRE MARNES A HUITRES C. DE SANNOIS ARGILE VERTE	ARGILE DE BOOM BERG / N.comta TONGEREN	HAMSTEAD BEDS	ASTRUP KASSEL RUPELTON / UNT. MEERESSAND MELANIENTON / LATDORF	CALC À ASTERIES	ST GEOURS PHARE GAAS A TALAYE
UPPER EOCENE	MARNES SUPRAGYPSEUSES GYPSE MARNES À P. ludensis	ASCHE	OYSTER MARLS BEMBRIDGE LST. HEADON BEDS BARTON BEDS	EOZÄN V	MARNES BLEUES	
MIDDLE EOCENE	SABLES MOYENS: MARINES CRESNES BEAUCHAMP AUVERS CALCAIRE GROSSIER	SABLES DE WEMMEL SABLES DE LÈDE SABLES DE BRUXELLES	UPPER BRACKLESHAM BEDS MIDDLE			

FIG. 1. Correlation of Mid-Tertiary Beds in western Europe.

I should like to record my grateful thanks to Prof. P. C. Sylvester-Bradley for his supervision throughout the work and for the use of the facilities of the Department of Geology at the University of Leicester. A study such as this also needs the cooperation of researchers in other countries, and I should particularly like to thank Dr H. J. Oertli, Mlle B. Deltel, the late Prof. J. Cuvillier, and Mme R. Damotte in France; Dr P. Marks in Holland; and Dr E. Triebel in Germany. The work was made possible by a N.E.R.C. NATO Research Studentship. The text-figures have been drawn by Mrs N. Farquharson.

The ostracods described in this paper are in the collections of the British Museum (Nat. History) Palaeontology Department.

II. LOCALITIES

Most of the samples used came from classical localities, either collected personally or donated by other workers. The sections are often poorly exposed, so few detailed measurements were taken. The relevant parts of some of the sections are given below. Other localities can be seen in Fig. 2.

1. Cormeilles-en-Parisis (P.C.M.).

This famous locality situated in the western suburbs of Paris reveals strata ranging from the marnes à *L. inornata*, through the gypsum beds, to the Couches de Sannois and Marnes à Huîtres at the top.

P.C.M.18–23;	Couches de Sannois, sandy clays with shell bands. The samples come from beds 40, 42, 44, 45, 46, and 47 respectively of Albissin (1955).
P.C.M.24;	basal Marnes à Huîtres.
P.C.M.25;	sandy clay 115 cm above base.
P.C.M.26;	oyster bed 230 cm above base.
P.C.M.27;	Brown clay with *Polymesoda* immediately above oyster bed.

2. Moiselles (PMS)

A sand pit beside the RN 1 some twenty miles north of Paris. Sables de Beauchamp, Sables d'Ezanville, and Calcaire de St. Ouen are exposed. Only one sample, PMS.8, has yielded well preserved *Cytheretta* species; this is from the Sables de Beauchamp, 480 cm below the base of the Sables d'Ezanville.

3. Marnes à *P. ludensis* of the Paris Basin.

Two localities yielded ostracods: Chavençon and Verzy. At both localities the Marnes à *P. ludensis* is thin; about 150 cm at Chavençon, PCC.1 near the base, PCC.2 100 cm above; about 90 cm at Verzy, PVY.2 at base, PVY.3 40 cm higher, PVY.4 30 cm higher still.

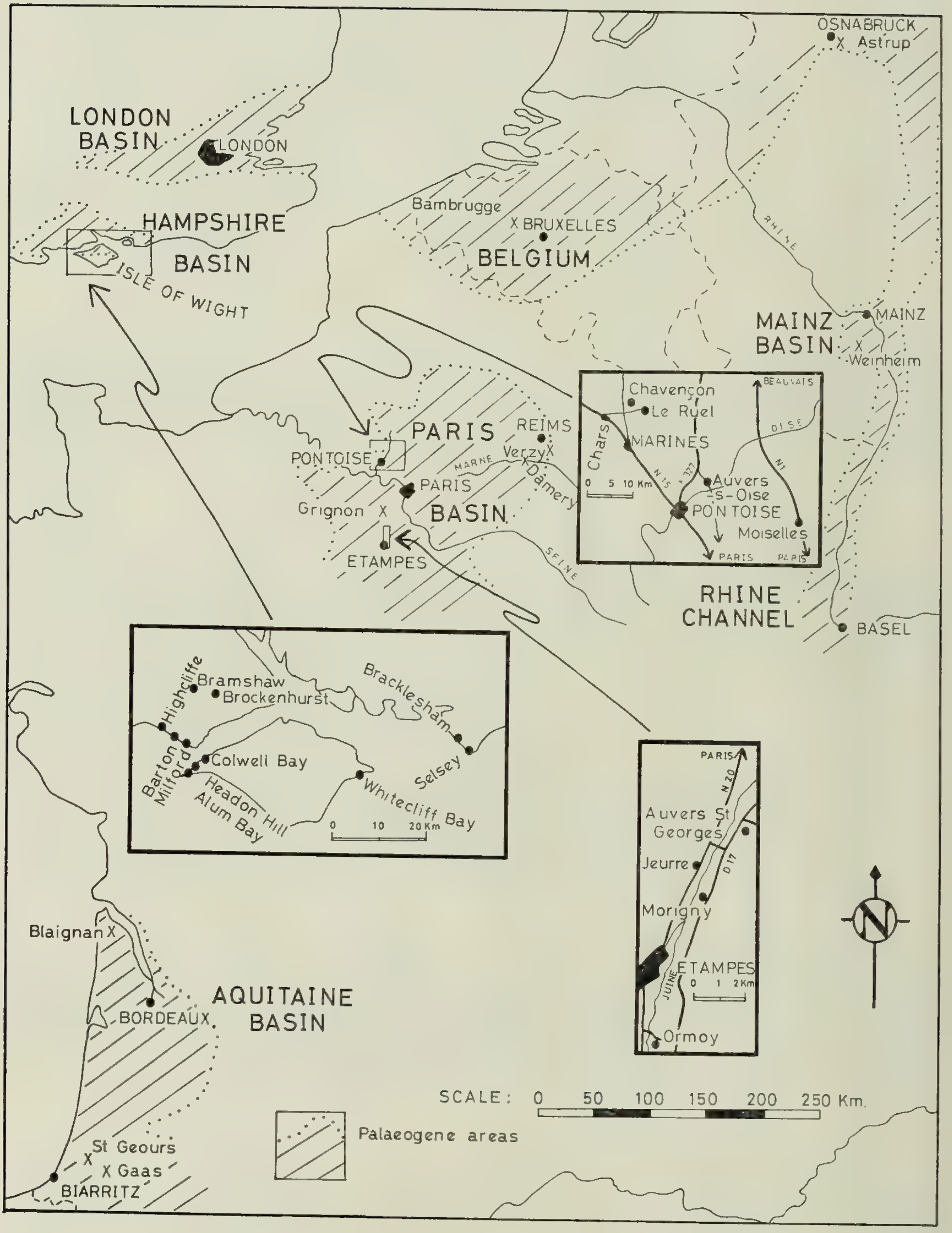
LONDON BASIN
LONDON
HAMPSHIRE BASIN
ISLE OF WIGHT
Bambrugge
X BRUXELLES
BELGIUM
OSNABRUCK
X Astrup
RHINE
MAINZ BASIN
MAINZ
X Weinheim
PARIS BASIN
REIMS
Verzy X
Damery
MARNE
PONTOISE
PARIS
Grignon X
ETAMPES
SEINE
Chavençon
Le Ruel
MARINES
Chars
0 5 10 Km
N 15
Auvers-s-Oise
PONTOISE
Moiselles
BEAUVAIS
OISE
N1
PARIS
PARIS
RHINE CHANNEL
BASEL
Bramshaw
Brockenhurst
Highcliffe
Barton
Milford
Colwell Bay
Headon Hill
Alum Bay
Bracklesham
Selsey
Whitecliff Bay
0 10 20 Km
PARIS
N 20
Auvers St Georges
Jeurre
D 17
Morigny
ETAMPES
JUINE
0 1 2 Km
Ormoy
N
Blaignan X
BORDEAUX
AQUITAINE BASIN
St Geours X
X Gaas
BIARRITZ
SCALE: 0 50 100 150 200 250 Km.
▨ Palaeogene areas

FIG. 2. Localities sampled for Cytherettinae.

4. Biarritz (RO).

The cliff section at Biarritz exposes strata ranging from the Lutetian to the upper part of the Oligocene. *Cytheretta* species are described from the following samples, collected at the foot of the cliffs. No detailed section was measured.

RO 264; base of the Couches de l'Atalaye.
RO 265; entrance to the tunnel at the Musée de la Mer.
RO 266; southern end of the Grande Plage.
RO 267; Rochers de la Villa Eugenie.
RO 268; southern end of the Falaise lou Cout.
RO 269, 270, 271; in ascending order below the Phare St Martin, collected over about 10 m of strata.

5. Other localities in the Aquitaine Basin.

(a) Bartonian clays of Lespontes.

(b) Stampian of Gaas. Two localities were sampled, Espibos (AGE) and Lesbarritz (AGL). The former of these is a completely overgrown quarry, where two samples were collected by digging, AGE.1 being slightly lower on the slopes than AGE.2. At Lesbarritz, AGL.1 was from the cream marls exposed at the base of the section below the coral horizon.

(c) St Geours de Maremne. The controversial locality at Escornbéou, which is of topmost Oligocene or lowermost Miocene age.

6. Headon Beds of the Hampshire Basin.

About 100 samples were examined; all cytherettinid species come from the Middle Headon Beds. Samples mentioned in the text are: Headon Hill, EHH.42, coming 165 cm above the base of the Venus Bed; Whitecliff Bay, EWB(A) from the base of the Brockenhurst Beds, EWB(B) 10 cm higher, EWB.19 from 100 cm above the top of the Barren Sands, and EWB.22 100 cm above EWB.19. Other localities sampled are Colwell Bay, Milford, and Brockenhurst.

7. Other localities.

Bracklesham Beds of Selsey Bill, Whitecliff Bay, and Bramshaw.

Auversian of Auvers-sur-Oise, and Le Ruel.

Stampian of Auvers-St-George, St Cloud, Ormoy, and Morigny in the Paris Basin, and of Weinheim Trift in the Mainz Basin.

Upper Oligocene of Astrup, near Osnabruck.

Ledian of Bambrugge, Belgium.

III. STRATIGRAPHICAL DISTRIBUTION

The genus *Cytheretta* is probably the commonest ostracod genus found in the mid-Tertiary of north-west Europe. It often forms up to 30% of the ostracod fauna, with an average of about 15%. The earliest species so far known is *C. nerva* Apostolescu. This was originally described from the Sables de Bracheux (Thanetian) of the Paris Basin, but has since been recorded as the subspecies *C. nerva montensis* Marlière from the Montian of Belgium and Dutch Limburg (Marlière, 1958; Deroo, 1966). *C. multicostata* Apostolescu is also found in the Sables de Bracheux. Other species are known from the London Clay (Ypresian) of the London and Hampshire

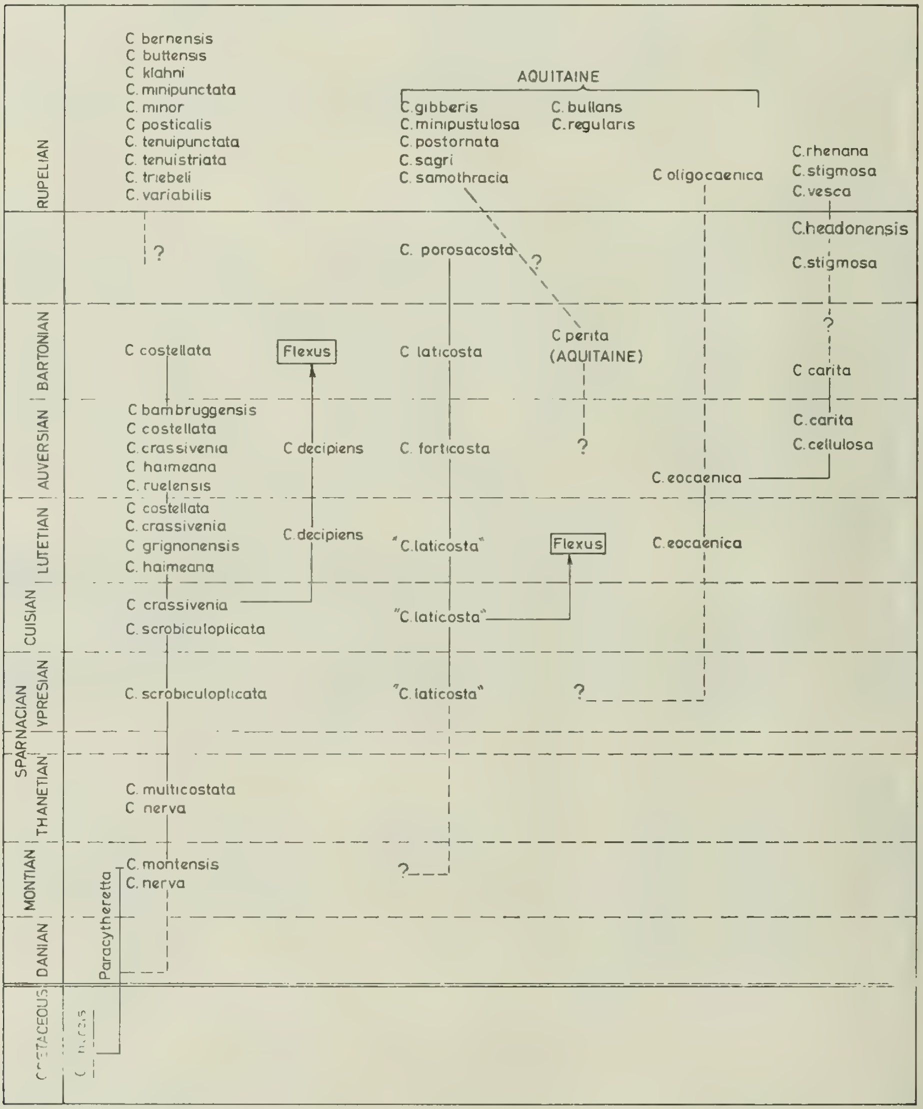
RUPELIAN
BARTONIAN
AUVERSIAN
LUTETIAN
CUISIAN
SPARNACIAN
YPRESIAN
THANETIAN
MONTIAN
DANIAN
CRETACEOUS
C bernensis
C buttensis
C klahni
C. minipunctata
C. minor
C posticalis
C. tenuipunctata
C. tenuistriata
C. triebeli
C. variabilis
AQUITAINE
C. gibberis
C. minipustulosa
C. postornata
C. sagri
C. samothracia
C. bullans
C. regularis
C oligocaenica
C. rhenana
C. stigmosa
C. vesca
?
C. porosacosta
?
C. headonensis
C. stigmosa
C costellata
Flexus
C laticosta
C perita
(AQUITAINE)
?
C carita
C bambruggensis
C costellata
C. crassivenia
C haimeana
C. ruelensis
C decipiens
C. forticosta
?
C. carita
C. cellulosa
C. eocaenica
C costellata
C. crassivenia
C grignonensis
C. haimeana
C. decipiens
"C. laticosta"
Flexus
C. eocaenica
C crassivenia
C. scrobiculoplicata
"C. laticosta"
C. scrobiculoplicata
"C. laticosta"
?
C. multicostata
C nerva
C. montensis
C. nerva
?
Paracytheretta

FIG. 3. Suggested lineages of *Cytheretta* in northwest Europe.

basins (Jones 1956; Haskins, 1968; Eagar, 1965) and from the Sables de Cuise of the Paris Basin (Keij, 1957; Apostolescu, 1964). It is clear that *Cytheretta* is found near the beginning of the Tertiary, and it is necessary to look into the Cretaceous for its ancestry.

The related genus *Paracytheretta* Triebel ranges from the Senonian to the Palaeocene (Morkhoven, 1963); the type species *P. reticosa* Triebel was described from the Middle Palaeocene of Denmark. Deroo (1966) has described four genera belonging to the subfamily from the Maastrichtian of Dutch Limburg. These include two new genera which are discussed in more detail below. Puri's statement (1958) that *Cytheretta* stemmed from *Paracytheretta* late in Palaeocene times therefore needs some modification. It would appear that the genus as now understood probably arose polyphyletically from late Cretaceous forms. Unfortunately Palaeocene and Lower Eocene species are not very well known, nor are Danian relatives, so it is impossible to discuss the origins of *Cytheretta* in any detail. It is not present in the well studied Maastrichtian faunas, but is in the Montian. The genus probably originated in western Europe, where it is most abundant, but it was already present in the Caribbean region during the Palaeocene (van den Bold, 1957), and also in Greenland (Szczezechura, 1971).

Two distinct lineages can be seen amongst the early forms of *Cytheretta* (Fig. 3). The first is the superspecies *C. laticosta* (Reuss) which is found throughout the Eocene. The second is the more complicated group which includes *C. nerva*, *C. scrobiculoplicata* (Jones), *C. crassivenia* Apostolescu, *C. costellata* (Roemer), *C. bambruggensis* Keij, *C. decipiens* Keij, *C. grignonensis* Apostoiescu and *C. haimeana* (Bosquet). The last six of these are Middle Eocene species, although *C. crassivenia* is also known from the Sables de Cuise (Lower Eocene). It was during Lutetian times that the group underwent a great explosion, both in numbers and in geographical range. Several are found in the Auversian (Sables d'Auvers, Sables de Beauchamp), but apart from *C. costellata* did not survive into the Bartonian. The Upper Eocene was essentially a period during which the descendants of the Middle Eocene radiation continued to evolve. Compared with the Middle Eocene, the number of species is poor but individuals are abundant. A third group emerged during the Middle Eocene, exemplified by *C. eocaenica* Keij. The history of this group is fragmentary. Its ancestors are unknown; it is not found in the Upper Eocene of the region, yet in the Lower Oligocene of Aquitaine *C. oligocaenica* sp. nov. is found which is so close in morphology as to be separable only with difficulty from *C. eocaenica*. It is possible that this group was ancestral to the Oligocene groups and to the Miocene and Recent species of the Mediterranean.

There were two distinct provinces in the Anglo-Paris region during the Eocene. The London Clay (Ypresian) of the western part of the London Basin has so far yielded only one common member of the genus, *C. scrobiculoplicata*, which is often extremely abundant (Eagar, personal communication). Bowen (1953) records one specimen of the *C. laticosta* group from Enborne, in the south-west London Basin. No younger species are known, however, because of the unfossiliferous nature of the succeeding strata. The London Clay of the Hampshire Basin also contains *C. scrobiculoplicata*, together with early members of the superspecies *C. laticosta*

(Haskins, 1968). For the remainder of the Eocene the superspecies *C. laticosta* is by far the most abundant *Cytheretta.* It is joined by *C. haimeana, C. costellata,* and *C. eocaenica* during the Middle Eocene, but in the Upper Eocene in most samples examined it is almost the sole representative of the genus. The Paris Basin formed the other province. During the Middle Eocene the *C. haimeana* group was common, no particular species being predominant; in the Upper Eocene however, *C. costellata* became completely dominant. In Belgium the picture is not clear, but it is apparently similar to the Paris Basin, although *C. eocaenica* is by far the commonest species in the Sable de Lède (Ledian).

There was a certain amount of communication between these regions, because *C. costellata* is occasionally found in the Barton Clay (Bartonian) of the Hampshire Basin, while the superspecies *C. laticosta* is present in the Paris Basin and Belgium. The communication was much clearer during the Middle Eocene than during the Upper Eocene.

The Oligocene saw an almost complete replacement of the Eocene species. New groups such as the superspecies *C. tenuipunctata* and *C. sagri* are dominant. The only groups with known Eocene ancestors are *C. rhenana* Triebel, *C. stigmosa* Triebel, and *C. oligocaenica.* The first two are related to species from the Headon Beds of the Hampshire Basin, *C. headonensis* Haskins and *C.* aff. *stigmosa* Triebel, which in turn are probably related to *C. eocaenica.* *C. oligocaenica* is also related to the Middle Eocene *C. eocaenica.* This reflects the general situation amongst the ostracods, i.e. at the base of the Oligocene a completely new fauna is found in western Europe. Provinces existed, as in the Eocene, but with a different constitution owing to palaeogeographical changes. The Paris Basin, Belgium, Mainz Basin, Rhine Graben and Swiss Basins formed one unit, and Aquitaine another. Within these are found sub-provinces due to geographical separation with the attendant evolution of distinct sub-species.

The genus *Flexus* Neviani is first reported from the Sables de Cuise (Cuisian) of the Paris Basin (Apostolescu, 1964). *Cytheretta decipiens* was placed in the genus *Flexus* by Puri (1958), but for reasons given below it is here retained in *Cytheretta.* However, this was probably the ancestor of *F. concinnus* (Triebel) (Keij, 1957; and see below). An undescribed species of *Flexus* has been observed in the Lutetian (Fisher Bed VII) of Whitecliff Bay, which is thought to have been derived from an early member of the superspecies *C. laticosta.* The genus is fairly common, though never abundant, in the Upper Eocene; it is represented by *F. solentensis* sp. nov. and *F. ludensis* sp. nov., the origins of which are unknown. In the Oligocene the genus is represented by *F. concinnus*; the type species *F. plicatus* (von Munster) comes from the Chattian. As used here, the genus is undoubtedly polyphyletic.

IV. EVOLUTION OF MID-TERTIARY CYTHERETTINAE

Various types of evolutionary pattern were exhibited by the Cytherettinae during Tertiary times. The *C. haimeana* species group is a good example of cladogenesis as defined by Sylvester-Bradley (1962). Using his terminology (Fig. 4) it is possible to recognize a first period of stabilization in the Palaeocene and Ypresian. During

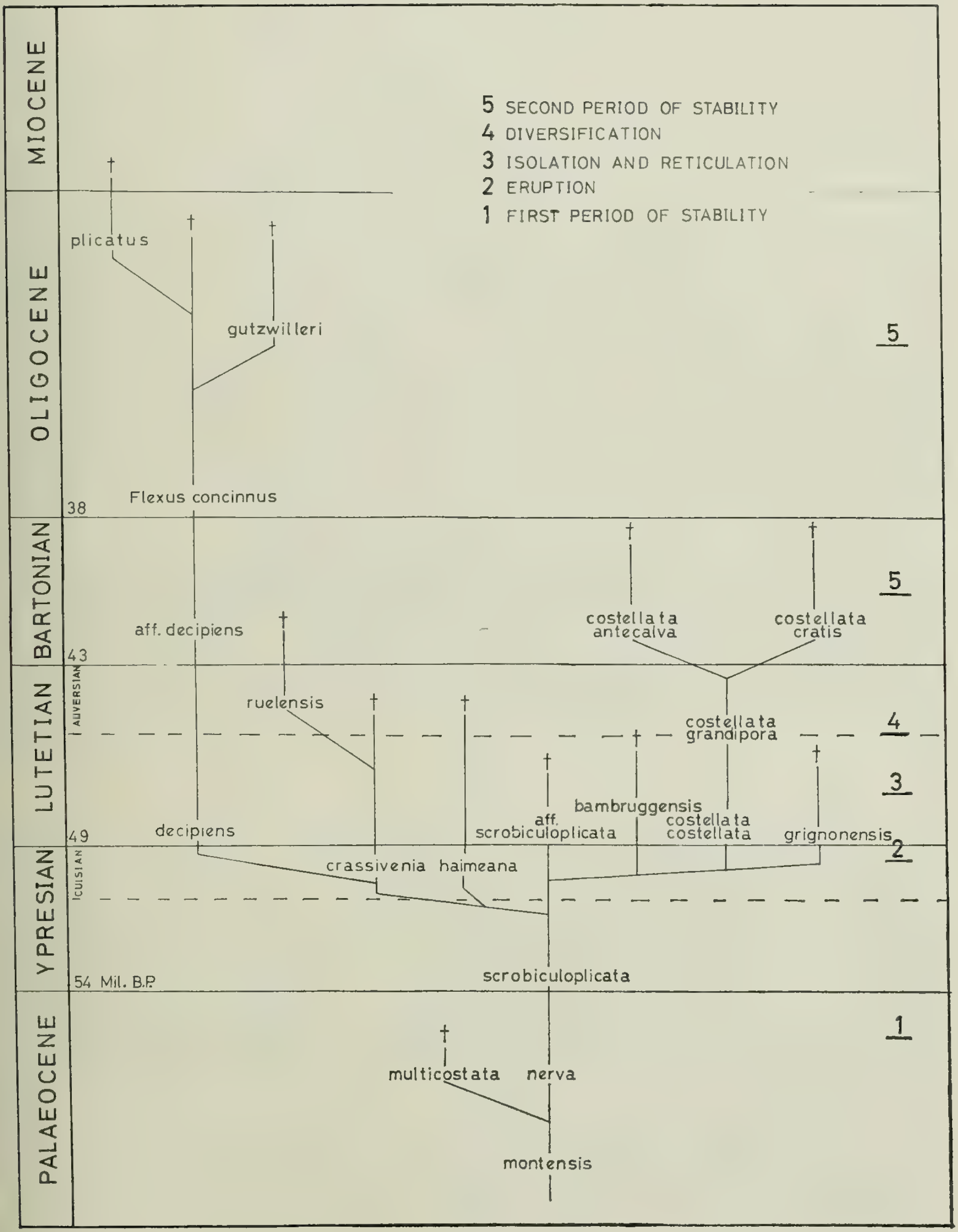
MIOCENE
OLIGOCENE
BARTONIAN
LUTETIAN
AUVERSIAN
YPRESIAN
CUISIAN
PALAEOCENE
5 SECOND PERIOD OF STABILITY
4 DIVERSIFICATION
3 ISOLATION AND RETICULATION
2 ERUPTION
1 FIRST PERIOD OF STABILITY
plicatus
gutzwilleri
38
Flexus concinnus
5
aff. decipiens
costellata antecalva
costellata cratis
5
43
ruelensis
costellata grandipora
4
3
bambruggensis
aff. scrobiculoplicata
costellata costellata
grignonensis
2
49
decipiens
crassivenia
haimeana
54 Mil. B.P.
scrobiculoplicata
1
multicostata
nerva
montensis

FIG. 4. The evolution of the *C. haimeana* species group.

this lengthy period, gradual evolution (stasigenesis) was taking place whereby *C. montensis* gave rise to *C. nerva*, which in turn led to *C. scrobiculoplicata*. In the Upper Ypresian (=Cuisian) a period of eruption began which continued into the Lutetian. During this period seven new species appeared. Perhaps significantly this coincided with a transgression of the sea, giving large areas of shallow marine waters ideal for *Cytheretta*, and presumably leading to a reduction in the selection pressure. The Middle Eocene (Lutetian and Auversian) was a time of extreme variation, and by the end of the Auversian most of the species were extinct. The Bartonian saw a second period of stabilization, with two geographical subspecies of *C. costellata*, and the descendants of *C. decipiens* which were now almost generically distinct. *Flexus* s.s. appeared in the Oligocene, representing the last members of the group. Final extinction occurred in the Quaternary. Within the species group the evolution of the subspecies of *C. costellata* shows a pattern very similar to the classic *Zaphrentis delanouei* as interpreted by Sylvester-Bradley (1951). In the Lutetian, *C. costellata costellata* consisted almost entirely of one morphotype; great variation occurred in the Auversian, with seven morphotypes, followed by stabilisation in the Bartonian where the subspecies consist mainly of one morphotype in each geographical region.

As opposed to this pattern, the superspecies *C. laticosta* shows gradual evolutionary change, without any period of explosive evolution.

A second period of eruption of the Cytherettinae occurred near the base of the Oligocene, once again coinciding with the spread of shallow seas over much of Europe. The superspecies *C. tenuipunctata* shows great eruption in the Lower Rupelian, with the presence of many geographical subspecies. This was followed by stabilization in the Upper Rupelian and Chattian.

Specific examples of evolution are dealt with in the taxonomic descriptions. These are *C. costellata*, *C. eocaenica*, *C. laticosta*, *C. buttensis*, *C. sagri*, and *F. solentensis*.

V. ECOLOGICAL DISTRIBUTION OF RECENT SPECIES

Three species are known from the Mediterranean:

C. judaea (Brady) the type species, is described by Kruit (1955) from the marine, shallow water (5–15 m), sandy deposits of the Rhone delta; Puri, Bonaduce & Malloy (1965) report it being found in association with *Posidonia* meadows in shallow banks around the islands and peninsulars of the Gulf of Naples, where the salinity is about 38%₀ and the bottom water temperature 14–15°C; Rome records it from the shallow waters at Monaco (0–3 m) associated with *Posidonia*; Ascoli (1965) found it in waters up to 74 m deep in the Adriatic Sea. Brady originally recorded it from the coast of Syria.

C. adriatica Ruggieri is apparently more restricted, but no details are available; it is found in beach sands at Rimini associated with *C. judaea*.

C. belgica (Brady) is reported by Kruit (1955) from the marine, sandy sediments of the Rhone delta in water of 10–15 m depth. These specimens may however be identical to *C. adriatica*.

Three species are present around the coasts of southern North America from the Bahamas, Florida, the Gulf coast and New York. These are *C. edwardsi* (Cushman), *C. sahni* Puri and *C. tracyi* Blake. *C. sahni* is reported by Hulings and Puri (1965) from a sand mud mixture in water less than 65 ft deep and with a salinity greater then 30‰. No details are known for the other two.

In the same region two species of *Protocytheretta* are present:

P. daniana Brady is reported by Puri and Hulings (1957) from clastic sediments at depths of 36–65 ft, more commonly in the deeper part; salinity, 28–35·6‰, clear water, temperature between 10° and 30°C; it is absent in the carbonate province of Florida. Curtis (1960) found it in sands, silts, and clays, particularly in water with an estuarine influence but predominantly marine; temperature 24–25°C. Kornicker (1965) mentions that it is found around the Bahamas.

P. multicarinata Swain was recorded by Swain (1955) from the nearshore Gulf of Mexico.

Cytheretta knysnaensis Benson is recorded by Benson & Maddocks (1964) from the Knysna estuary, South Africa, where it is found in muddy sands free from wave action but with a fair current; salinity is 28·4‰, pH 8; it is associated with a partly marine and partly estuarine fauna. However, following the description of this species there are reasons for believing it may not be a true *Cytheretta*; the inner margin, radial pore canals and central muscle scars are different, there is a vestibule and an internal eye sinus, which *Cytheretta* does not have.

To sum up, *Cytheretta* is normally found in shallow (10–30 m) nearshore clear waters of normal salinity; the temperature is warm ('Mediterranean') with a bottom water temperature of about 15°C; the substratum is a sand or sandy clay, often covered with seaweed. The genus *Protocytheretta* seems to be able to tolerate slightly brackish conditions with a salinity as low as 28‰.

VI. PALAEOECOLOGY

The genus undoubtedly inhabited a similar environment during the Eocene as the recent species. This accounts for its abundance in the Tertiary of the Paris Basin, London Basin, Hampshire Basin, Belgium, Mainz Basin and the Swiss basins. These were all shallow water areas, except for the eastern part of the London Basin where the genus has not been recorded so far. The clear distinction between the London and Hampshire basins on the one hand and the Paris Basin on the other is probably in part geographical and in part related to the contrast between the sediments of the two regions. In the former the ostracods are mainly found in argillaceous deposits, while they are found in arenaceous and calcareous deposits in the latter.

The Upper Eocene of Biarritz has yielded only one or two specimens of *Cytheretta*, while *Cytherella* and *Pontocyprella* are extremely abundant. On the other hand, some inland exposures contain fairly abundant *Cytheretta*. The Oligocene of Biarritz also contains abundant *Cytheretta*. This is undoubtedly ecologically controlled. The Upper Eocene saw deep water at Biarritz which shallowed eastwards, eventually giving way to continental deposits; at the end of the Eocene the water shallowed with a change from argillaceous to arenaceous deposition.

The Headon Beds of the Hampshire Basin contain sediments deposited in a variety of environments ranging from freshwater to shallow marine. Ostracods are found in most of these environments, but *Cytheretta* is restricted to the marine phases; as soon as brackish conditions prevailed *Cytheretta* disappeared. Thus it is found in association with such genera as *Pterygocythereis*, *Trachyleberidea*, *Bradleya*, *Leguminocythereis*, *Brachycythere* and *Haplocytheridea*. Whenever such genera as *Neocyprideis* or *Cytheromorpha* become abundant, *Cytheretta* is no longer present.

VII. GEOGRAPHICAL DISTRIBUTION

Fossil species have so far been reported from the Palaeocene, Eocene, Oligocene, Miocene, Pliocene and Quaternary of Europe; from the Palaeocene, Eocene, Oligocene, and Miocene of North America and from the Palaeocene of Greenland (Szczechura, 1971); Latham (1938) recorded *Cytheretta costellata* (Roemer) from the salt range, Punjab, but this is a misidentification and is probably a species of *Buntonia*. In space *Cytheretta* would appear to be restricted to the coasts of the North Atlantic and adjacent seas; the case of the South African *C. kysnaensis* has already been mentioned. Its greatest development is in Europe, where some hundred species, both fossil and recent, have been described.

Flexus has only been reported from western Europe where it ranges from the Lower Eocene to the Quaternary, the latest recorded species being *F. triebeli* Ruggieri from the Upper Pliocene and Lower Quaternary of Italy (Ruggieri, 1952).

Protocytheretta is restricted to North America where it ranges from the Oligocene to Recent. It is found in the Gulf of Mexico, and also off the west coast of California and Mexico (Swain, 1969).

Recently described genera are mainly known from their type areas only. Thus *Acuticytheretta* and *Semicytheretta* are only known from western Europe, while *Bensonia*, *Grekoffiana*, and *Argenticytheretta* are only recorded from south America. For a discussion of these see the next section.

VIII. CLASSIFICATION OF THE SUBFAMILY CYTHERETTINAE

Following Hazel (1967) the Cytherettinae are regarded as a subfamily of the Trachyleberididae; this based on the muscle scars, hinge, and soft parts.

The following genera have been included by various authors within the subfamily: *Cytheretta* Muller, 1894; *Flexus* Neviani, 1928 (syn. *Eucytheretta* Puri, 1958); *Pseudocythereis* Skogsberg, 1928; *Buntonia* Howe, 1935; *Paracytheretta* Triebel, 1941; *Loculicytheretta* Ruggieri, 1954; *Ambocythere* Van den Bold, 1957; *Protocytheretta* Puri, 1958; *Netrocytheridea* Howe and Laurencich, 1958; *Neocytheretta* Morkhoven 1963; *Acuticytheretta* Deroo, 1966; *Semicytheretta* Deroo, 1966; *Bensonia* Garcia, 1969; *Grekkofiana* Garcia, 1969; and *Argenticytheretta* Garcia, 1969.

Loculicytheretta was placed in the subfamily by both Ruggieri (1954) and Howe (Treatise, 1961), but its distinctive characters would seem to exclude it. Deroo (1966) placed *Netrocytheridea* into the subfamily; however its shape and entomodont hinge would appear to exclude it. The only real similarity is in the irregular shape of the inner margin. *Ambocythere* was included by Morkhoven (1962, 3) because of its supposed ressemblance to *Buntonia*; its false radial pore canals, branching radial pore canals, and lateral shape do not support its inclusion. *Neocytheretta* from Indonesia is not considered to belong to the subfamily. It has eye spots (*Cytheretta* is blind), a completely different type of ornamentation, and a different hinge; only the irregular inner margin resembles *Cytheretta*.

Pseudocythereis was placed in the subfamily by Puri; no material has been available for study, only the original description of Skogsberg could be examined. The type species is *Cythereis* (*Pseudocythereis*) *spinifera* Skogsberg, and the author was undoubtedly comparing it with *C. rubra* Müller as far as the soft parts were concerned, but the description of the shell is inadequate. Therefore, no conclusion could be reached concerning it, except to agree with Puri that there are strong resemblances to *Cytheretta*.

Paracytheretta has a very well developed anterior hinge ear in the left valve and no other *Cytheretta* species approach it in this respect. The hinge is apparently similar to *Cytheretta* (Morkhoven, 1963), the surface of the valve is reticulate with three longitudinal ridges.

The development of three longitudinal ridges is a common feature of the subfamily, but not all such forms are necessarily closely genetically related. Puri recognized three such genera, *Paracytheretta*, *Eucytheretta*, and *Protocytheretta*. The latter was said to be *Cytheretta*-shaped, while the others were *Cythereis*-shaped; the first two were then differentiated on the hinge, which is *Cytheretta*-like in *Eucytheretta* and *Cythereis*-like in *Paracytheretta*. However, Triebel's original description of the hinge of *Paracytheretta*, as shown by Morkhoven (1963) is the same as for *Cytheretta*. There is, however, no doubt that *Paracytheretta* is a valid genus because of its distinctive shape. *Flexus* has a totally different shape, much more like that of *Cytheretta*. *Flexus* and *Protocytheretta* can be separated, both on shape and ornamentation. The only species studied that Puri placed into *Protocytheretta* is *P. schoelleri* Keij from the Oligo-Miocene of Aquitaine; apart from this species the genus would be restricted to North America. A study of descriptions and illustrations of *P. daniana*, the type species, suggests that *P. schoelleri* does not belong to the same genus, and therefore, that the genus is probably restricted to North America (see description and discussion in *P. schoelleri* below).

Flexus has already been shown to be polyphyletic. It is used here for all species shaped like the type species, *F. plicatus* (von Munster) and having three prominent longitudinal ridges. This is not a very satisfactory arrangement, but present knowledge makes it very difficult to divide it into new genera.

Similarly, no attempt has been made to further subdivide the genus *Cytheretta*. As mentioned above, there are six distinct groups in the Eocene and Lower Oligocene of western Europe. However, the recognition of such monophyletic groups is difficult to correlate with easily diagnosed morphological characteristics, so it has been thought better for the present to limit their taxonomic recognition to the rank of superspecies. Further investigation, particularly of Lower Tertiary forms, should lead to a phylogenetic division of the genus; this must be combined with a study of the American species, and so is beyond the scope of the present work.

The six groups mentioned above are:

- *C. haimeana* group
- *C. laticosta* group
- *C. eocaenica* group
- *C. tenuipunctata* group
- *C. sagri* group
- *C. rhenana* group

Acuticytheretta certainly has a *Cytheretta*-like appearance in general outline, has unequal valves and similar muscle scars to *Cytheretta*. The inner margin is very wide posteriorly, but not irregular; and the hinge is simpler, with a large anterior tooth in the right valve, and a small anterior tooth at the end of the smooth (?) bar of the left valve, and a posterior tooth in the right valve. It could represent a primitive member of the subfamily.

Semicytheretta has a similar hinge and muscle scars to *Cytheretta*, but has a narrow and regular inner margin and a different shape.

Deroo also describes *Cythere euglypha* Bosquet and *Cythereis euglyphoidea* Van Veen, which from the illustrations could also be included in the subfamily. Their shape, unequal valves, muscle scars, and ornamentation suggest this; the hinge has faintly crenulate anterior and posterior teeth in the right valve, and the inner margin is narrow and regular. They are placed in the genus *Anticythereis* Van den Bold. These could be early primitive members of the subfamily.

Morkhoven (1962, 3) included *Buntonia* in the subfamily because the first thoracic legs of the male are similar to those of *Cytheretta*. In general appearance certain *Buntonia* species can be confused with cytherettinids, although there are noticeable differences in the hinge and the inner margin. It is provisionally included within the subfamily.

Grekoffiana is described as being similar to *Protocytheretta*, but with a regular inner margin. The type species is *G. australis* Rossi de Garcia. In the discussion of the new genus (1969; 218), de Garcia placed *Protocytheretta daniana* (Brady) Benson and Coleman in *Grekoffiana*. This might be taken to imply the species as interpreted by Benson and Coleman, and not Brady's species; on page 220 we have mention of '*Grekoffiana daniana* (Brady) dans Benson et Coleman (1963) (p. 26, Tab. 5, Figs 5, 7, 9 & 10)'; again, perhaps implying the species as interpreted by Benson and Coleman, but in this case there should have been some statement to this effect. The idea is thus given that Brady's species is being included in the new genus, even though it is in fact the type species of *Protocytheretta*. *P. daniana* is generally thought of as having a typical cytherettinid sinuous inner margin, although following Benson and Coleman it may in fact show considerable variation. Thus two problems arise: firstly, if *P. daniana* can have a regular or a sinuous inner margin, i.e., it is an infra-specific character, it can hardly be used to diagnose a new genus; and secondly, the type species of a genus cannot be included in a new genus. There are grounds then for wondering whether *Grekoffiana* is in fact a valid genus, and not a synonym of *Protocytheretta*.

Bensonia is described as being similar to *Cytheretta*, but with a regular inner margin. The hinge and overall appearance certainly look like a typical cytherettinid. *Cytheretta knysnaensis* is placed in this genus, and as stated previously, there are certain features, particularly the implied presence of an eye, which would exclude it from *Cytheretta*. The presence or absence of any occular structures cannot be determined from Rossi de Garcia's description, so it is difficult to know whether *Bensonia* is a true cytherettinid genus. It is provisionally placed in the subfamily.

Argenticytheretta is illustrated with what appears to be an eye tubercle, and in overall shape does not resemble *Cytheretta*. It also has a regular inner margin.

From this it would seem that there exists a group of *Cytheretta*-like ostracods, principally occurring on the two sides of the south Atlantic, but which differ from true cytherettinids in several respects. Perhaps it is a case of homeomorphy? Until more species are described in detail, this question must remain unanswered.

The genera included within the subfamily are:

Cytheretta
Flexus (syn. *Eucytheretta*)
Paracytheretta
Protocytheretta (syn. *Grekoffiana*?)
Acuticytheretta
Semicytheretta
Provisionally: *Buntonia*
Pseudocythereis
Doubtfully: *Bensonia*
Argenticytheretta

The characters taken to be diagnostic of the Cytherettinae are: inequivalve, the left valve being markedly larger and differently shaped than the right; a modified holamphidont hinge; presence of a fulcral point; numerous and simple radial pore canals; generally sinuous inner margin; unornamented, or with a predominantly longitudinal ornamentation; development of few posterior spines and many anterior denticles; lack ot occular structures, lateral spines, and caudal process.

IX. THE SHELL STRUCTURE OF CYTHERETTA

Cytheretta typically has an elongate-ovate shape. The dorsal margin is straight to convex, often with a posterior hinge ear and sometimes with an anterior hinge ear in the left valve. The posterior margin is obliquely curved with a sharp, high postero-dorsal angle and a gentle slope round to the ventral margin. The latter is often concave, always so in the right valve. The valves are usually very unequal in size and shape, the left valve being much larger and with a greater height; in lateral view the outline of the left valve over-reaches that of the right valve in most places. This over-reach is particularly prominent in the postero-dorsal angle where the hinge ear is developed and in the anter-dorsal angle where the antero-dorsal lobe (see below) of the hinge of the left valve rests on the antero-dorsal platform of the right. The shape in dorsal view varies. Sexual dimorphism is distinct, the males being more elongate.

The carapace may be completely unornamented, as in the type species. More usual, however, is an elongate ornamentation which can take the form of either longitudinal rows of pits, usually better developed towards the posterior, or longitudinal ridges. The latter often have reticulation developed between them, and some ridges converge to form a sub-central plexus (Fig. 5). For descriptive purposes the ridges are numbered from the dorsal margin in a position just to the posterior of the sub-central plexus (Fig. 5). The anterior and antero-dorsal regions of both valves are often smooth, while the rest of the carapace is ornamented. The ornamentation is generally similar for both valves.

The hinge is modified holamphidont with several accessory elements (Fig. 6, 7; Plates 5, 7, 8). In the left valve there is an anterodorsal lobe, which is an outgrowth of the selvage and rests on to an antero-dorsal platform in the right valve. The anterior socket is partially opened ventrally; it is bordered by an antero-ventral lobe which fits into the modified anterior part of the anterior tooth of the right valve, the antero-ventral sinus, which is a hollow in the tooth. The antero-median tooth is generally small, the postero-median bar is crenulate and swollen at the posterior to give a postero-median swelling. This is sometimes almost as prominent as the antero-median tooth, as in the type species; it forms one edge of the posterior socket, which is almost open ventrally. The posterior socket often forms a posterior hinge ear, sometimes with a lobe. In the right valve the anterior tooth has an almost vertical face towards the anterior; it is sometimes stirpate (=stepped), or with a gentle posterior slope. In lateral view the tooth has a concavity in the antero-ventral position, the antero-ventral sulcus. The antero-median socket is shallow, the postero-median groove is crenulate, and there is usually a shallow postero-median socket. The posterior tooth is generally pessular (i.e. with more or less parallel sides) and is sometimes almost as prominent as the anterior tooth, as in the type species.

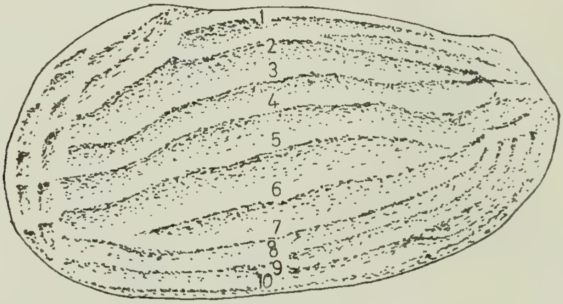

FIG. 5. *C. costellata* (Roemer), showing the system of numbering the ridges. ×75.

There is considerable variation in the details of the duplicature. The selvage is generally more prominent in the right valve. At the anterior it usually has a position close to the outer margin, but in some species it is further away so that a prominent flange groove is formed; there is a wide flange groove developed along the ventral margin of the right valve, with a narrow one along the posterior. The selvage is

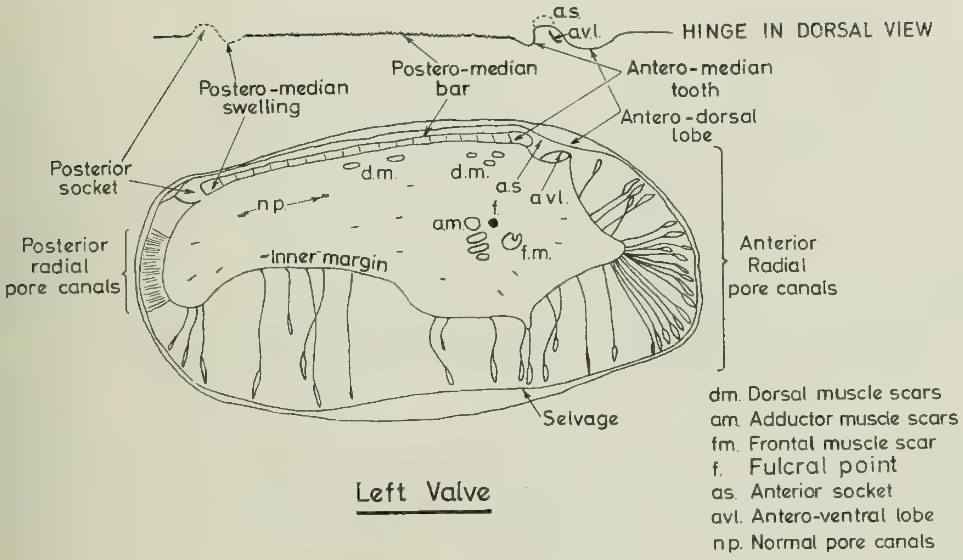
a.s.
a.v.l.
HINGE IN DORSAL VIEW
Postero-median swelling
Postero-median bar
Antero-median tooth
Antero-dorsal lobe
Posterior socket
d.m.
d.m.
a.s
a v l.
n p.
f.
am.
f.m.
Posterior radial pore canals
Inner margin
Anterior Radial pore canals
Selvage
Left Valve
dm. Dorsal muscle scars
am. Adductor muscle scars
fm. Frontal muscle scar
f. Fulcral point
as. Anterior socket
avl. Antero-ventral lobe
n p. Normal pore canals

FIG. 6. Internal structure of the left valve of *Cytheretta*.

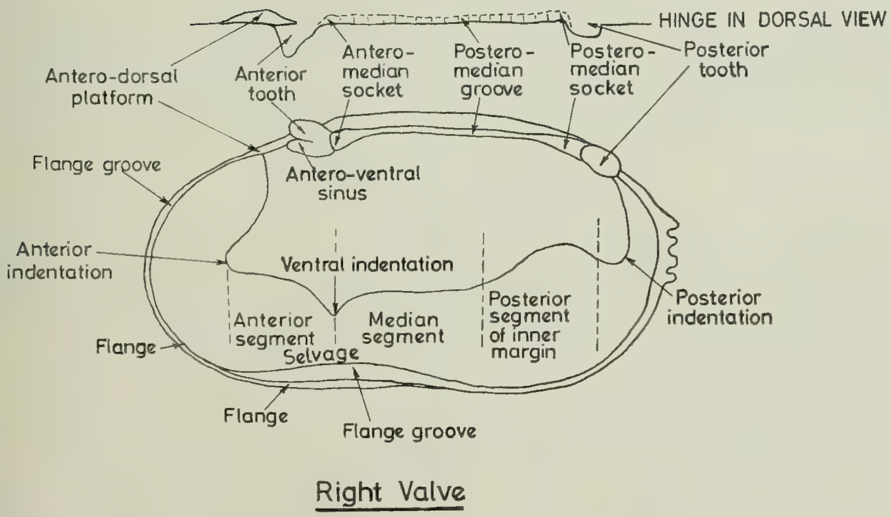
HINGE IN DORSAL VIEW
Antero-dorsal platform
Anterior tooth
Antero-median socket
Postero-median groove
Postero-median socket
Posterior tooth
Flange groove
Antero-ventral sinus
Anterior indentation
Ventral indentation
Anterior segment
Median segment
Posterior segment of inner margin
Posterior indentation
Flange
Selvage
Flange
Flange groove
Right Valve

FIG. 7. Internal structure of the right valve of *Cytheretta*.

sometimes very strongly developed at the posterior. The flange usually forms the outer margin. A weak list is often present.

The outline of the inner margin is a characteristic feature; it is broad with three principal indentations (Fig. 7); its outline can be divided into three segments for descriptive purposes. It ends against the anterior and posterior hinge elements. The anterior and ventral radial pore canals are long, simple, often crossing one another, usually bulbous near the outer margin (Pl. 1). The anterior pore canals tend to be concentrated around the antero-ventral angle. The posterior radial pore canals are rather different (Pl. 1, Fig. 9); the inner lamella in which they are situated is not fused to the outer lamella, so that a vestibule is in fact formed. The posterior radial pore canals are numerous, straight and very closely packed; often they form two groups, a ventral one of short pore canals similar to the anterior and ventral radial pore canals, and a dorsal one of closely packed pore canals.

The central group of muscle scars consists of a row of four adductors; the lower two often touch and the third one often elongate; and a large irregularly 'U'-shaped frontal scar with a smaller scar in front. A fulcral point is prominent, forming a raised boss; this feature is also a well known characteristic of the Cytherideinae (von Morkhoven, 1963). A dorsal group of about three muscle scars can be detected. There are two mandibular scars which almost touch, or one elongate scar near, and just anterior to, the ventral indentation (Pl. 1, Fig. 7).

There is no eye spot or occular sinus, as *Cytheretta* is blind. The feature often described as an eye spot is the antero-dorsal lobe of the hinge of the left valve.

X. SOFT PARTS

The soft parts have not been examined during this study, and the only published descriptions are for *C. rubra*, *C. edwardsi* (Cushman) 1906 and *C. tracyi* Blake, 1929 (Hazel, 1967). The principal characters 'are the three-jointed exopodite of the second antennae, absence of a seta on the posterior border of the protopodite of the first thoracic legs' (Hazel, 1967; 40, after Müller, 1894) and an asymmetry of the first pair of thoracic legs in the male which is developed to varying degrees.

XI. LARVAL STAGES

Only the last three larval stages have so far been recognized. They tend to be more triangular in shape, with a pointed posterior. Ornamentation in the last moult is similar to that of the adult, but in earlier moult stages is only partially developed. The hinge is very simple; in the left valve the antero-dorsal lobe is developed, followed by an anterior socket open ventrally, smooth bar and posterior socket, also opened ventrally; the corresponding features are present in the right valve.

About one in fifty of the adult specimens appears to be weakly calcified. The hinge is an adult hinge, but weak; the inner margin is straight, without the normal indentations, and very narrow. Pokorny (1965) suggested that such a feature might be due to a parasitic infection and Morkhoven (1963) that the animal died soon after moulting and before calcification was complete. Oertli (1965) mentions the case of

Faluna where the true adult form is very rare, and the thinly calcified moult stage was probably mature, i.e. a case of neotony. Sandberg (1965) supported this by citing cases where such immature forms contained eggs. However, in the case of *Cytheretta* Morkhoven's explanation is probably the correct one.

In two species, *C. eocaenica* and *C. oligocaenica*, a few very large specimens are found. They are about double the size of the normal adult, but otherwise identical. This is a fairly frequent phenomenon in several families of the Ostracoda. Benson (1965) suggests that such forms might be a gerontic stage; and Kesling in the Treatise (1961) considers that they represent post-maturation instars.

XII. THE SHELL STRUCTURE OF FLEXUS

Internal details are the same as for *Cytheretta*. As defined here, all *Cytheretta*-like forms with three prominent longitudinal ridges are referred to this genus.

XIII. THE TYPE SPECIES OF CYTHERETTA

Müller described *Cytheretta* in 1894 with *C. rubra* Müller as type species. In 1950 Ruggieri put *C. rubra* into the synonymy of *C. subradiosa* (Roemer), originally described from the Pliocene of Italy. This was accepted by Triebel (1952), Puri (1958) and Hazel (1967), but queried by Morkhoven (1963). Thanks to Prof. Ruggieri, who kindly supplied the material, it has been possible to study both forms. Morkhoven also mentioned that *C. rubra* might be a synonym of *Ilyobates*? *judaea* Brady, 1868; Hazel accepted this view, but places both *C. rubra* and *C. judaea* within the synonymy of *C. subradiosa*. Fortunately Brady's material is preserved in the collections of the Hancock Museum, No. B67, presently under the care of Dr. K. McKenzie. There is no doubt that *C. judaea* is the senior synonym. The problem now is whether this is synonymous with *C. subradiosa*.

C. subradiosa was described from the Pliocene of northern Italy at Castellarquato; none of Roemer's material is available for study, but Ruggieri has obtained topotype material. The specimens described below come from the Pliocene of San Arcangelo, near Rimini. Müller's specimens were from the Gulf of Naples; the specimens described below come from the beach sand at Rimini.

A comparison of the Pliocene specimens with the recent has shown a number of differences which are believed to distinguish *C. judaea* from *C. subradiosa*. The position of the Quaternary forms is unknown.

The major difference is in the line of the inner margin, particularly the posterior segment. In *C. judaea* this cannot be separated from the median segment, but in *C. subradiosa* it is steep, giving a narrow and deep posterior indentation; the posterior indentation in *C. judaea* is very broad. There are more radial pore canals in *C. subradiosa*, 32 compared with 24 in *C. judaea*. The central muscle scars are situated more to the dorsal in *C. subradiosa*; the four adductors are larger and the frontal is more dorsally situated in respect to the adductors. There is a slight difference in shape in that *C. judaea* is more obliquely rounded in the anterior margin. The hinge is almost identical although the anterior tooth of the right valve is slightly more prominent in *C. judaea*.

Finally, Müller included two distinct species in his description of *C. rubra* (see below). One is probably synonymous with *C. judaea* and the other with *Cytheridea striatopunctata* Terquem 1878.

XIV. SYSTEMATIC DESCRIPTIONS

Subclass *OSTRACODA* Latreille, 1806

Order PODOCOPIDA Müller, 1894

Suborder PODOCOPINA Sars, 1866

Family **TRACHYLEBERIDIDAE** Sylvester-Bradley, 1948

Subfamily **CYTHERETTINAE** Triebel, 1952

Genus ***CYTHERETTA*** Müller, 1894

1894 *Cytheretta* Müller, p. 382
1906 *Pseudocytheretta* Cushman, p. 382
1928 *Cylindrus* Neviani, p. 106
1941 *Prionocytheretta* Mehes, p. 60

Diagnosis: The carapace is elongate-ovate, with a gently curving postero-ventral angle so that the posterior margin is markedly asymmetrical. Generally very inequivalve, with a large left valve. Ornamentation consists of longitudinal ridges or rows of pits, or the carapace may be smooth. The hinge is modified holamphidont. The line of inner margin is sinuous; the duplicature is wide; selvage, flange, and list are developed to varying extents; the radial pore canals are simple, long, bulbous, and curved; the normal pore canals are simple. The central muscle scars consist of a row of four adductors and a large irregularly 'U'-shaped frontal; a fulcral point is well developed.

Type species: *Ilyobates*? *judaea* Brady.

Discussion: The type species of *Cylindrus* is *C. jurinei* (von Munster) which is a true *Cytheretta*; the name *Cylindrus* is also preoccupied (Fitzinger, 1833, Mollusca). Neither of the other two have been studied; Puri (1958) states that the shell structure of *Pseudocytheretta* is identical with that of *Cytheretta*, and Hazel (1967) discusses the genus in some detail and concludes that it is synonymous with *Cytheretta*. Triebel (1952) places *Prionocytheretta* in the synonymy of *Cytheretta*.

Cytheretta judaea (Brady)

(Pl. 1, fig. 1, 4–7, 9; Text Fig. 8)

1868 *Ilyobates ? judaea* Brady: 112, pl. 13, figs 17, 18.
1894 *Cytheretta rubra* Müller: 382, pl. 8, figs. 9, 10, 16; pl. 39, figs 8–22, 24.
1912 *Cytheretta rubra* Müller; Müller: 366.
1950 *Cytheretta subradiosa* (non. Roemer; pars); Ruggieri: 9.
1953 *Cytheretta subradiosa* (non. Roemer; pars); Ruggieri: 102.
1955 *Cytheretta rubra* Müller; Kruit: 482, pl. 5, figs 9a–c.
1958 *Cytheretta subradiosa* (non. Roemer; pars); Puri: 186, pl. 1, figs 3–7.
1959 *Cytheretta subradiosa* (non. Roemer; pars); Ruggieri: 190.

DIAGNOSIS: A species of *Cytheretta* with sub-parallel dorsal and ventral margins and unornamented surface. The inner margin is almost straight.

MATERIAL: Thirteen valves and carapaces from the beach sand at Rimini; Io 3792–4; 3810.

TYPE LOCALITY AND HORIZON: Haifa, Recent.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Recent—Rhone delta, Monaco, Naples, Adriatic Sea, Syria, Aegean Sea; Quaternary of Italy?

DESCRIPTION: Sexual dimorphism is not strong; the males are more elongate. Sex ratio 1·5. The left valve has a weak posterior hinge ear; the dorsal margin is slightly convex; the anterior margin is strongly obliquely rounded. The ventral margin is almost straight and roughly parallel to the dorsal margin; the posterior margin is obliquely rounded. The greatest height is just to the posterior of centre. The ventral margin of the right valve is concave. In dorsal view the carapace is ovate, tapered towards the anterior.

The shell is smooth, but with conspicuous opaque areas; there is a large one in the central region and a smaller one in the anterior. These are approximately constant in position in all specimens, producing the black areas seen in Pl. 1, fig. 4.

The antero-dorsal lobe of the hinge of the left valve is flat; the postero-median swelling is pronounced. In the right valve the posterior tooth is almost equal in prominence to the anterior tooth.

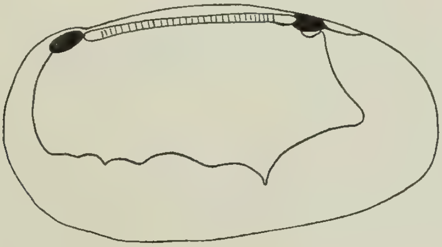

FIG. 8. *Cytheretta judaea* (Brady); left valve; ×75.

The anterior indentation of the inner margin is wide and downward pointing; the anterior segment is gently curved; the median and posterior segments cannot be separated; the posterior segment is large and broadly rounded. There are some 24 anterior, 27 ventral, and 32 posterior radial pore canals. The posterior set can be divided into two groups; a ventral group of ten, widely spaced and bulbous, and a dorsal group of 22, very close together and straight. There are some 25 scattered normal pore canals. The selvage is close to the outer margin, with a flange groove along the ventral margin.

Dimensions:

	Left valve			Right valve			Carapace
	L	H	L/H	L	H	L/H	W
Female	0·75	0·43	1·74	0·75	0·40	1·88	0·42
Male	0·79	0·43	1·84	0·78	0·39	2·00	0·40

Discussion: Müller (pl. 8, fig. 13) and Puri (pl. 1, figs 9–13) illustrate large specimens with longitudinal rows of puncta. These must represent a different species; as well as the differences already mentioned, the anterior margin is much squarer than the obliquely rounded *C. judaea*. Triebel (1952; 17) suggests that these belong to *Cytheridea striatopunctata* Terquem, described by Terquem (1878) from the Pliocene of Rhodes. Several specimens of this type were found in the sample from Rimini, and were first thought to belong to *C. adriatica* Ruggieri; however, none have such strong longitudinal ridges as those illustrated by Puri (1958, pl. 2, figs 1–5). They are perhaps members of a gradational series in which *C. adriatica* represents the morphotype with the strongest developed ornamentation.

See also the generic discussion (p. 281).

Cytheretta subradiosa (Roemer)

(Pl. 1, fig. 8)

1838 *Cytherina subradiosa* Roemer: 517, pl. vi, fig. 20.
1880 *Cytherella calabra* Seguenza: 326, 366, pl. 17, fig. 56.
1900 *Cytheridea subradiosa* (Roemer); Namias: 105, pl. 15, fig. 17.
1905 *Bairdia subradiosa* (Roemer); Cappelli: 306, pl. 9, fig. 4.
1928a *Cytheridea subradiosa* (Roemer); Neviani : 66.
1928b *Cytheridea subradiosa* (Roemer); Neviani: 131.
1950 *Cytheretta subradiosa* (Roemer); Ruggieri; 9–11 (pars).
1953 *Cytheretta subradiosa* (Roemer); Ruggieri: 102 (pars)
1959 *Cytheretta subradiosa* (Roemer); Ruggieri: 190 (pars).

Diagnosis: An unornamented species of *Cytheretta* with sub-parallel dorsal and ventral margins. The inner margin has a steep posterior segment.

Material: Five carapaces and valves, together with several fragments, from the Lower Pliocene of San Arcangelo, near Rimini. Io 3795.

Type locality and horizon: Castellarquato; Pliocene.

Stratigraphical range and distribution: Pliocene of Sicily, Calabria, Castellarquato, and Rimini; Quaternary of Italy?

DESCRIPTION: The left valve has a very weak posterior hinge ear; the dorsal margin is almost straight, although in some specimens there is a distinct convexity in the central region which interrupts the smoothness of the margin. The anterior margin is obliquely rounded. The ventral margin is straight in the presumed females, but concave in the one specimen thought to be a male. The posterior margin is broadly rounded. The right valve has a greater height towards the posterior; the ventral margin is concave. The carapace is ovate in dorsal view.

The shell is smooth, with no ornamentation.

The hinge of the left valve has a flat antero-dorsal lobe; the antero-ventral lobe is weak; the postero-median swelling is pronounced and equal in size to the antero-median tooth. In the right valve the posterior and anterior teeth are equal in size.

The anterior indentation of the inner margin is wide and downward pointing; the ventral indentation has a flat base instead of the usual 'V' shape; the posterior indentation is narrow, deep and curved. The anterior segment is almost straight; the median segment is slightly irregular, with a gentle upward slope towards the posterior; the posterior segment is very steep. There are some 32 anterior, 34 ventral, and 32 posterior radial pore canals; and 25 scattered normal pore canals. The selvage runs very close to the margin; there is a small flange groove along the ventral margin.

DIMENSIONS: Carapace

	L	H	W	L/H
Female	0·75	0·45	0·37	1·67
Male	0·81	0·44	0·36	1·84

DISCUSSION: From the few specimens studied, there would appear to be considerable variation in shape. See also the generic discussion (p. 281).

Cytheretta costellata (Roemer)

DIAGNOSIS: A species of *Cytheretta* with a characteristic ornamentation of ten longitudinal ridges which unite and bifurcate in a regular pattern; posterior margin with four strong spines, anterior margin with some nine denticles. Strongly inequivalve. Duplicature with an anterior flange groove and a ventral list.

DESCRIPTION: Seven morphotypes have been recognized, chiefly on ornamentation. These are described below.

The ornamentation consists of ten longitudinal ridges with varying ornamentation between (see Text-fig. 5). The second ridge bifurcates towards the posterior and the lower part eventually joins ridge no. 3; from the junction a thin ridge runs into no. 4. Ridge no. 4 is prominent, and forms the dorsal limit to the subcentral plexus towards the anterior. No. 5 forms the ventral limit and again is prominent; in the posterior of the valve it joins no. 7. No. 6 appears to be enclosed between 5 and 7, and joins one of these two. No. 7 is very prominent and extends further towards the posterior than any other; 8 and 9 join together in a position level with the sub-central plexus, 9 bifurcating just to the posterior. An area of reticulation of varying size is present at the anterior.

The antero-dorsal lobe of the hinge of the left valve is swollen; the antero-ventral lobe is poorly developed; the antero-median tooth is prominent and downward pointing; the postero-median swelling is pronounced but small in comparison with the antero-median tooth; the posterior socket is circular rather than ovate.

There are some 30 anterior pore canals, about 30 very closely packed posterior radial pore canals, and 15 ventral radial pore canals. The selvage is prominent; a flange groove is present, particularly prominent in the right valve, both anterior and posterior. Four spines come from the flange at the posterior and some 9 denticles are developed along an anterior fringe. A faint list is developed, particularly along the ventral side.

The central muscle scars are in a slight pit; they are small, the two ventral scars close together, the third elongate, and the dorsal-most scar circular.

Sexual dimorphism is pronounced; sex ratio 1·75.

Discussion (I): Roemer (1838) originally described the species from the Tertiary of the Paris Basin; the specimen illustrated has six ridges and four or five posterior spines. Its shape is similar to the Lutetian forms of the species to be described below. Bosquet (1852) recorded it from the Sables infèrieurs, Calcaire grossier, and the sables moyens; it was commonest in the Calcaire grossier. His diagram shows eight ridges and four spines. Keij (1957) redetermined Bosquet's material and records several species and genera amongst it. Roemer's material is thought to be lost and Keij's revision of Bosquet's material has been followed in the interpretation of the species. There is, therefore, still some doubt about the identity of Roemer's

LOCALITY	MORPHOTYPES							SUBSPECIES
	A	B	C	D	E	F	G	
BARTON (7)	-	-	-	-	-	14·3	85·7	antecalva
CHAVENCON (109)	-	-	-	-	-	100	-	cratis
VERZY (162)	-	-	-	-	-	100	-	
LE RUEL (7)	-	-	-	28·6	42·9	14·3	14·3	grandipora
MOISELLES (52)	15·4	1·9	7·7	15·4	59·6	-	-	
AUVERS (20)	45·0	15·0	5·0	15·0	20·0	-	-	
BRACKLESHAM (97)	100	-	-	-	-	-	-	costellata
DAMERY (61)	100	-	-	-	-	-	-	

Fig. 9. Morphotypes and subspecies of *C. costellata* (Roemer).
The numbers in brackets refer to the number of specimens examined.

species. Bosquet (1852) mentions Roemer in his acknowledgments for supplying material however. Jones and Sherborn's new variety *C. costellata* var. *triangulata* from the type Bracklesham Beds is a female dimorph.

Amongst the material studied it is possible to recognize seven morphotypes which fall into four groupings, here recognized as subspecies. Three of these are chronological subspecies and the fourth is geographical. (Text-fig. 9). For a discussion of the subspecies as used here see Sylvester-Bradley 1951.

Morphotype A:

The left valve, particularly of the female, is triangular with its apex at the anterior; the dorsal margin is gently convex with a prominent posterior hinge ear; the ventral margin is slightly convex, sweeping round at the posterior in a continuous curve to form the ventral part of the posterior margin; the dorsal part of the posterior margin turns sharply round to meet the hinge ear. The anterior margin is obliquely rounded. The right valve is much lower than the left with a strongly convex dorsal margin and a concave ventral margin. In dorsal view the carapace is ovate.

The ornamentation between the ridges consists of a fine punctation. In the anterior part of the valve the ridges tend to become submerged within a large area of reticulation. A strong marginal rim runs around the anterior and dorsal margins. The sub-central plexus is simple. Ridge no. 6 is joined at both ends to no. 7 by a fine thread-like continuation.

The outline of the inner margin differs slightly between the two valves. The anterior indentation is small and pointed; the anterior segment slopes down quite steeply to the small and ill-defined ventral indentation. In the left valve the median segment is at first level and then slopes upwards to the posterior segment, where the slope steepens markedly and sweeps up close to the dorsal margin; then it curves sharply downwards to form a deep and narrow posterior indentation. In the right valve the median segment is entirely level. In the males the posterior segment reaches much closer to the ventral margin.

Morphotype B:

Similar in most respects to Morphotype A. However, a very strong and characteristic sub-central plexus is developed, especially well seen in a specimen from Bambrugge (Pl. 2, fig. 5). It consists of a raised platform between ridges 4 and 5 with three pits on its surface. This is a character developed in all the remaining morphotypes and is generally very prominent. The shape is slightly different to Morphotype A as the ventral margin is more convex and so the carapace appears to be much less triangular.

Morphotype C:

The shape of this and the remaining morphotypes is similar to that of Morphotype B but with the development of an anterior hinge ear in the left valve.

The ornamentation between the ridges consists of a punctation intermediate in size between that of Morphotype A and that of Morphotype F. This and the remaining morphotypes show a slight difference in ornamentation between the two valves. In the left valve ridge no. 6, joins No. 7 in the anterior but ends without joining either 5 or 7 at the posterior; in the right valve of some specimens ridge no. 7 bifurcates near the posterior margin, the dorsal branch is joined by no. 5 and the ventral branch joins no. 8. There is a prominent sub-central plexus. The anterior area of reticulation is much reduced compared with Morphotypes A and B.

Morphotype D:

Large pits are developed between the longitudinal ridges, but can only be seen by straining. The pits are not developed in the posterior regions and cover a larger area of the valve in some specimens than in others. Other features are similar to Morphotype E.

Morphotype E:

This has a strong development of large pits between the ridges. The large pits are two abreast between the median portions of ridges no. 3 and 4, and in this respect Morphotype E differs from Morphotype F, which has a network of small pits. Ridges 5 and 7 join in the posterior, leaving an unattached no. 6 between them. The anterior area of reticulation is smaller than in Morphotype A, but larger than in Morphotype F.

Morphotype F:

The anterior margin is evenly rounded and in this respect differs from Morphotypes A–E. Pitting is developed between the ridges; the pits are large between ridges 3–7, but form a network of small pits between 1, 2, and 3. The anterior area of reticulation is narrow, only two reticules wide; this results in the longitudinal ridges being more prominent in the anterior region than in Morphotypes A–E. The sub-central plexus is prominent. In the left valve ridge no. 5 is the strongest at the posterior and 6 and 7 join it; a few examples can be seen where no. 5 joins no. 7, and a few in which the ridges do not join at all. In the right valve no. 7 bifurcates near the posterior, the dorsal portion usually joining 5 and the ventral portion joining 8. This pattern is also present in a few left valves.

The inner margin differs from that of Morphotypes A–E; the posterior segment is not so steep and does not reach so far towards the dorsal margin; the posterior indentation is therefore not so deep.

Morphotype G:

This is similar to Morphotype F except for the development of a smooth area at the anterior. This varies in extent; in some specimens it is small, in others it extends almost to the sub-central plexus. Both males and females are affected. In the left valve ridge no. 5 is the most prominent at the posterior; no. 6 joins 5 or 7 or neither. The right valve is similar to that of Morphotype F.

Cytheretta costellata costellata (Roemer)

(Pl. 2, fig. 1–10)

1838 *Cytherina costellata* Roemer: 517, pl. 6, fig. 24.
1852 *Cythere costellata* (Roemer); Bosquet: 58 (pars), pl. 2, fig. 11.
1857 *Cythere costellata* (Roemer); Jones: 32, pl. 5, fig. 11.
1874 *Cythere costellata* (Roemer); Brady, Crosskey and Robertson: 152, pl. 16, figs 13–15.
1889 *Cythere costellata* (Roemer) var. *triangulata* Jones and Sherborn: 30, pl. 1, fig. 21.
1955 *Cytheretta costellata* (Roemer); Apostolescu: 26, pl. 5, figs 75, 76.
1957 *Cytheretta costellata* (Roemer); Keij: 132, pl. 22, fig. 7.

DIAGNOSIS: A subspecies of *C. costellata* with fine puncta between the ridges and usually with a simple sub-central plexus.

MATERIAL: Material was examined from the following localities; Lutetian IV of Damery, Fisher Beds 21–24 of Selsey, the Keij Collection at Utrecht (Belgian Lutetian and Ledian), Ledian of Bambrugge. For numbers see Text-fig. 9. Io 3796–3803.

TYPE LOCALITY AND HORIZON: Lutetian of the Paris Basin.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: See Text-fig. 10.

DESCRIPTION: This is composed of Morphotypes A, B, and C. It is small in size (see Text-fig. 11 and Discussion II).

REMARKS: The Ledian specimens at Utrecht have not been included in Text-fig. 9 because these were only measured and not divided into morphotypes. Most of them are Morphotype A; a few show very faint pitting in places and are therefore Morphotype D. The specimens mentioned by Keij (1957; 133) as being reticulate are not *C. costellata*.

Cytheretta costellata grandipora subsp. nov.

(Pl. 3, figs 1–8)

1852 *Cythere costellata*; Bosquet: 58 (pars).
1957 *Cytheretta costellata* (Roemer); Keij: 132 (pars), pl. 6, fig. 9.

DERIVATION OF NAME: Latin—grandis, large, and pora, pit; refers to the large pits developed between the ridges.

DIAGNOSIS: A subspecies of *C. costellata* characterized by the presence of large pits between the longitudinal ridges with a well developed sub-central plexus.

HOLOTYPE: Io 3804, a female left valve.

PARATYPES: Io 3805, 3806, 3808–9, 3811–13.

MATERIAL: See Text-fig. 9.

TYPE LOCALITY AND HORIZON: Carrière de Moiselles, Sables de Beauchamp.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Sables d'Auvers, Auvers-sur-Oise; Sables de Beauchamp, Moiselles; Sables de Cresnes, Le Ruel. All are in the Paris Basin.

Description: This consists of Morphotypes A-G, but principally A–E; thus there is a great range in ornamentation and size. For size, see Text-figs 9 and 10.

Cytheretta costellata cratis subsp. nov.

(Pl. 4, figs 1–8; Pl. 5, figs 1–3. Text-fig. 5)

Derivation of name: Latin—cratis, wickerwork; refers to the ornamentation.

Diagnosis: A subspecies of *C. costellata* characterized by the development of pits between the ridges and a narrow area of reticulation at the anterior.

Holotype: Io 3814, a female left valve.

Paratypes: Io 3815–3822.

Material: See Text-fig. 9.

Type locality and horizon: Verzy; Marnes à *P. ludensis*.

Stratigraphical range and distribution: Marnes à *P. ludensis* of Verzy and Chavençon in the Paris Basin.

Description: This consists entirely of Morphotype F. For dimensions see Text-fig. 11.

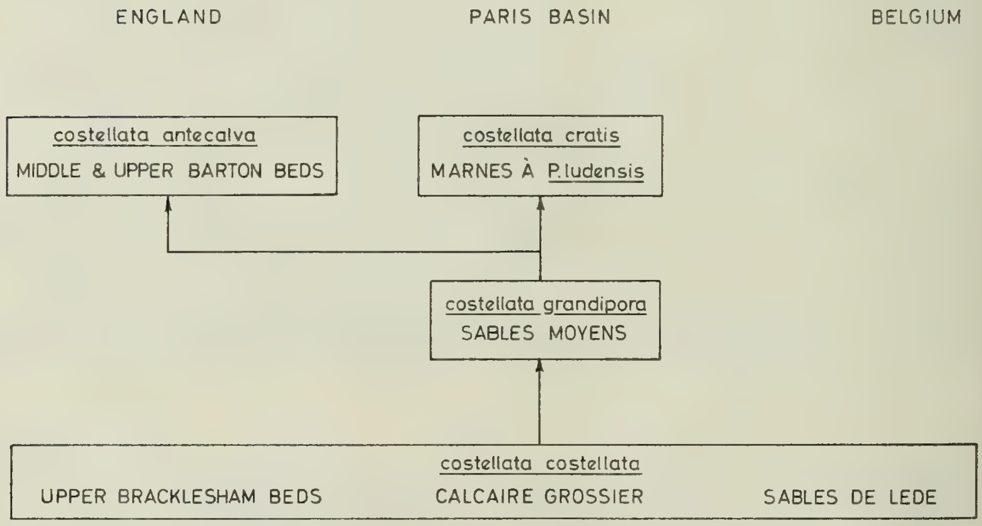
ENGLAND
PARIS BASIN
BELGIUM
costellata antecalva
MIDDLE & UPPER BARTON BEDS
costellata cratis
MARNES À P. ludensis
costellata grandipora
SABLES MOYENS
costellata costellata
UPPER BRACKLESHAM BEDS
CALCAIRE GROSSIER
SABLES DE LEDE

Fig. 10. Stratigraphical and geographical distribution of the subspecies of *C. costellata* (Roemer).

Cytheretta costellata antecalva subsp. nov.

(Pl. 4, figs 9–11)

1968 *Cytheretta costellata* (Roemer); Haskins: 165; Pl. 2, fig. 1–8.

Derivation of name: Latin—ante, anterior, and calvus, smooth; refers to the smooth anterior region.

Diagnosis: A subspecies of *C. costellata* characterized by a smooth area at the anterior; pits are present between the longitudinal ridges.

Holotype: Io 3823, a female left valve.

Paratypes: Io 3824–6.

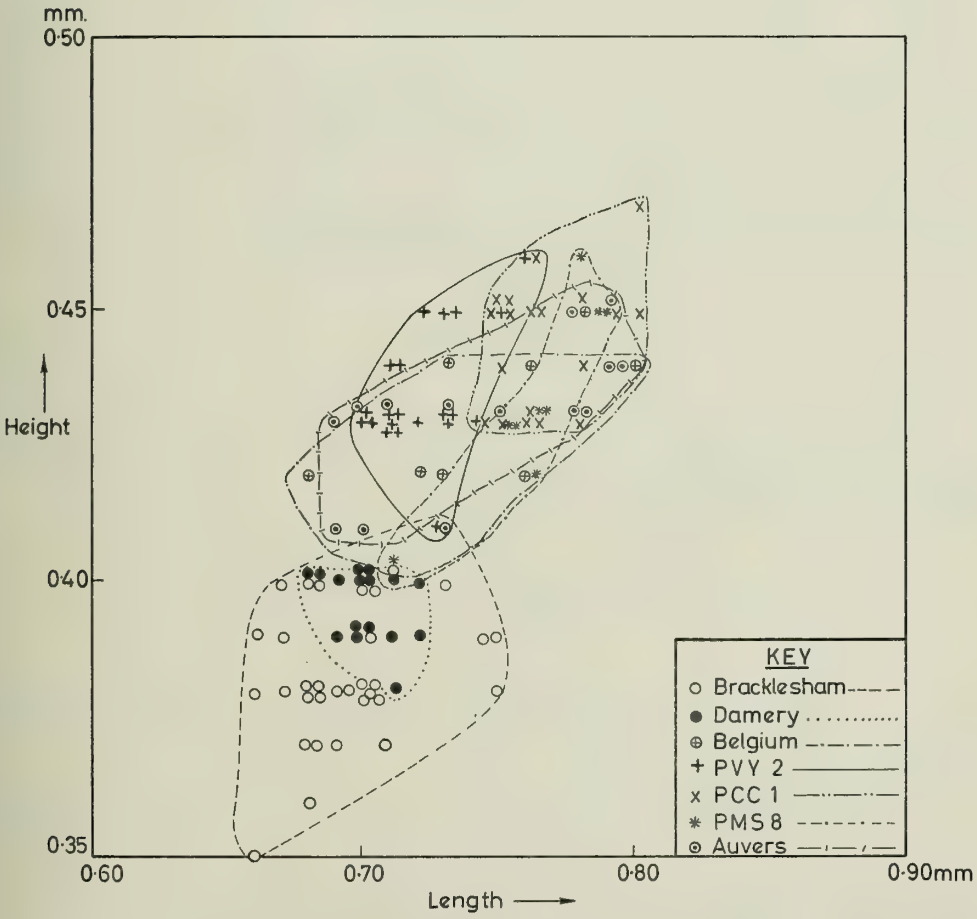

Fig. 11. Size distribution of *C. costellata* (Roemer). PVY=Verzy; PCC=Chavencon; PMS=Moiselles.

Type locality and horizon: Barton; Upper Barton Beds, Bed H (Chama Bed).

Stratigraphical range and distribution: Middle and Upper Barton Beds, Barton; Middle Barton Beds, Alum Bay.

Description: This consists of Morphotypes F and G, but mainly the latter.

Dimensions: Holotype, L=0·77 mm.

Remarks: Although the number of specimens is small, a further set of specimens was described by Haskins (1968) from Alum Bay which also had a smooth anterior region, so that this is apparently a well marked character.

Discussion (II): Each assemblage studied shows a range of variation, indicated rather crudely by the proportion of morphotypes it contains. In fact gradations between morphotypes occur and the division into discrete groups is therefore arbitrary. The differences between subspecies are marked by changes in the proportion of the constituent morphotypes. Most of these changes can be correlated with stratigraphical position, but in the case of *C. costellata cratis* subsp. nov. and *C. costellata antecalva* subsp. nov. it seems probable that we are dealing with contemporary subspecies that are geographically separated. The suggested relationships between the subspecies of *C. costellata* are shown in Text-fig. 10.

In general there is an increase in size with time. This is clearly seen in Text-figs 11 & 12. A comparison between the morphotypes found at Auvers and Moiselles (Text-fig. 12) shows that Morphotype A tends to be the smallest and E the largest.

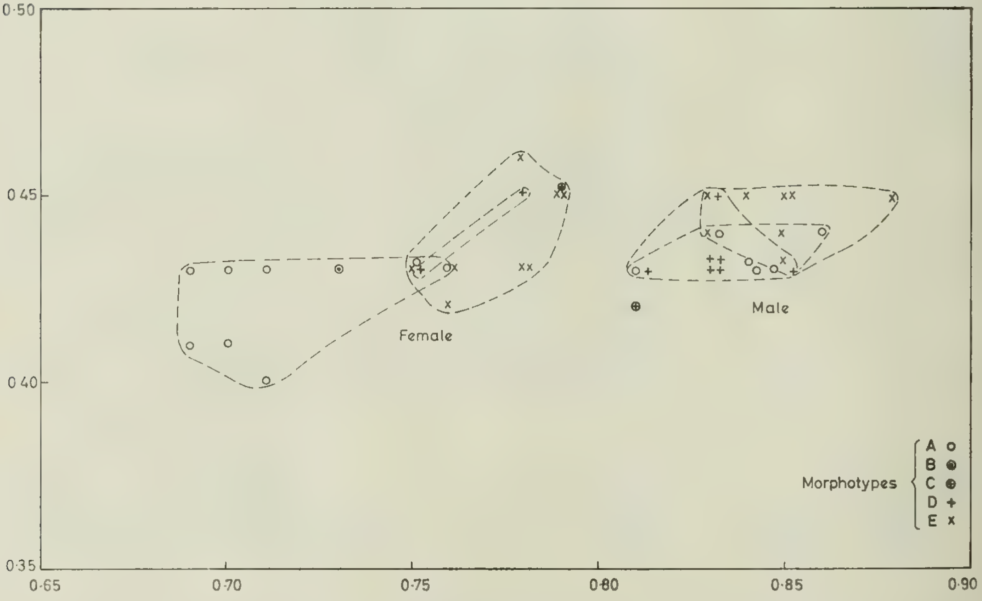

Fig. 12. Size distribution of morphotypes of *C. costellata* (Roemer) from Auvers-sur-Oise.

This is much clearer in the case of the females than the males. The species from Verzy are smaller than those from Chavençon; as these are of the same age, and because most other ostracods are similarly affected, this is thought to be ecologically controlled. The specimens from the Belgian Sable de Lède are much larger than those from Damery and Bracklesham.

The ridge pattern remains remarkably constant, apart from the posterior involvement between ridges nos. 5, 6 and 7. With time there is an increase in complication of the ornamentation between the ridges and a decrease in the width of the anterior area of reticulation. At the posterior ridge no. 7 is at first the most prominent and no. 5 and 6 join it; this changes until no. 5 is the strongest and no. 6 and 7 join it (Text-fig. 13).

The anterior margin changes from obliquely rounded to evenly rounded. The Ludian forms are proportionally higher than the Lutetian ones.

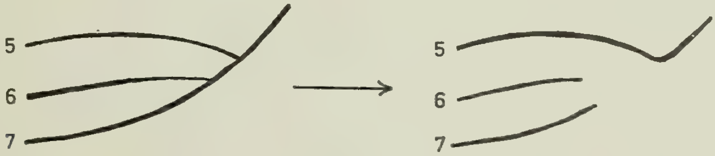

FIG. 13. Changes in ridges 5, 6 and 7 of C. costellata (Roemer).

Cytheretta bambruggensis Keij

(Pl. 3, fig. 9)

1957 *Cytheretta bambruggensis* Keij: 131, pl. 6, fig. 10, pl. 10, figs 9–11.

MATERIAL: One right valve from the Sables de Lède of Bambrugge. Io 3827.

TYPE LOCALITY AND HORIZON: Bambrugge (Belgium); Sables de Lède.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Lutetian, Ledian and basal Sables de Wemmel, Belgium; 'Bartonian' of the borehole at Delden, the Netherlands.

Cytheretta crassivenia Apostolescu

(Pl. 6, figs 2, 5)

1852 *Cythere costellata* (non Roemer; pars); Bosquet: 58.
1955 *Cytheretta crassivenia* Apostolescu: 261, pl. 5, figs 77–79.
1957 *Cytheretta crassivenia* Apostolescu; Keij: pl. 6, fig. 4; pl. 10, figs 12–14.

MATERIAL: Two valves from the Lutetian of Grignon; nine valves and carapaces from the Lutetian of Damery; two carapaces from the type Sables d'Auvers; eleven valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3828, 9.

TYPE LOCALITY AND HORIZON: Montmirail; Lutetian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Lutetian, Sables d'Auvers of the type locality, Sables de Beauchamp of Moiselles in the Paris Basin; Sables de Lède of Belgium.

Discussion: Ridge no. 4 is strong and runs from the anterior to the posterior; beneath it are two short, but conspicuous ridges. In the specimens from Grignon and Damery (Lutetian) these two ridges do not quite join, the anterior one finishing just above the anterior end of the posterior ridge; in the specimens from Moiselles, however, they actually join. The reticulation between the ridges tends to be slightly stronger in the Moiselles specimens than in the Lutetian ones.

Cytheretta decipiens Keij

(Pl. 6, figs 8–10)

1955 *Cytheretta concinna* (non. Triebel) Apostolescu: 261, pl. 4, figs 72–74.
1957 *Cytheretta decipiens* Keij: 133, pl. 6, fig. 8, pl. 10, figs 15–16.

Material: One carapace from the type Sables d'Auvers, five valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3830–32.

Type locality and horizon: Forest (Belgium), Cuisian.

Stratigraphical range and distribution: Cuisian, Lutetian and Ledian of Belgium; Lutetian, Sables d'Auvers, and Sables de Beauchamp of the Paris Basin.

Discussion: It has been decided to retain this in the genus *Cytheretta* rather than *Flexus* because of the presence of several minor longitudinal ridges, apart from the three main ones. The ridge pattern is, in fact, very similar to that of *C. crassivenia* and also to *C. haimeana*, *C. scrobiculoplicata* and *C. bambruggensis*. If Keij's supposition is correct, i.e. *C. decipiens* was the ancestor of *Flexus concinnus* (Triebel), at least some part of the genus *Flexus* has clearly been derived from Middle Eocene *Cytheretta*. The transition can be closely placed to the Bartonian.

Cytheretta aff. ***decipiens*** Keij

(Pl. 6, fig. 3)

Material: One carapace from the Marnes à *P. ludensis* at Chavençon. Io 3833.

Dimensions: L, 0·66; H, 0·34; L/H, 1·94.

Discussion: This is clearly related to *C. decipiens*, but has lost most of the minor longitudinal ridges; there are still several ventral ridges however. This is probably the form called *C. concinnus* by Keij, but it differs from the latter in several respects. However, it could be placed in an evolutionary sequence, which, starting with *C. decipiens*, eventually gave rise to *F. concinnus*. As only one specimen was available for study, this question has been left open.

Cytheretta haimeana (Bosquet)

(Pl. 6, figs 1, 6)

1852 *Cythere haimeana* Bosquet: 61, pl. 2, fig. 14.
1852 *Cythere costellata* (non. Roemer) Bosquet (pars): 58.
1955 *Cytheretta haimeana* (Bosquet); Apostolescu: 262, pl. 5, figs 84–85.
1957 *Cytheretta haimeana* (Bosquet); Keij: 136, pl. 6, fig. 7, pl. 10, figs 7, 8.

MATERIAL: One valve from the Lutetian of Damery; ten valves and carapaces from the type Upper Bracklesham Beds; five valves and carapaces from the type Sables d'Auvers; eight valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3834–5.

TYPE LOCALITY AND HORIZON: Grignon; Lutetian IV.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Cuisian and Lutetian of the Paris Basin (numerous localities) and the type Sables d'Auvers and Sables de Beauchamp of Moiselles; Upper Bracklesham Beds of England.

DISCUSSION: The specimens from Moiselles and Auvers are larger than those from Damery. The longitudinal ridges are more prominent because the cross ridges are not so strongly developed as in the Lutetian forms.

Cytheretta ruelensis sp. nov.

(Pl. 6, figs 4, 7; Pl. 5, figs 4–7)

DERIVATION OF NAME: From the hamlet of Le Ruel.

DIAGNOSIS: A species of Cytheretta with 12 longitudinal ridges, of which no. 4 and 5 are prominent, and with coarse puncta between the ridges.

HOLOTYPE: Io 3837, a female left valve.

PARATYPE: Io 3838.

MATERIAL: Four carapaces and one left valve.

TYPE LOCALITY AND HORIZON: Le Ruel; Sables de Cresnes.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: So far only known from the type locality.

DESCRIPTION: Sexual dimorphism is very distinct, the males being more elongate. The left valve has an almost straight dorsal margin with a prominent posterior hinge ear. The anterior margin is obliquely rounded; the ventral margin is almost straight; the posterior margin is obliquely rounded. The right valve has a convex dorsal margin and a concave ventral margin. The carapace is narrowly ovate in dorsal view.

The ornamentation consists of 12 longitudinal ridges with coarse puncta between them. Ridge no. 1 forms most of the dorsal margin, leaving it towards the anterior where it swings downwards to join a narrow anterior area of reticulation. Ridges 2 and 3 are not strong; towards the posterior no. 2 bifurcates and no. 3 joins the lower and stronger part. No. 4 and 5 are very strong running almost the whole length of the carapace; a prominent gap is developed between them to the posterior of the sub-central plexus. The sub-central plexus is not very well developed and lies between ridges 4 and 5. There are four rows of coarse puncta between ridges 4 and 5 forming two double rows; there are four more closely packed rows between 3 and 4; two between 2 and 3, and 5 and 6; and one between the remaining ridges.

The internal features could not be clearly seen.

DIMENSIONS (Carapace):

	L	H	L/H	W
Female	0·75	0·43	1·74	0·35
Male	0·85	0·44	1·93	0·37

DISCUSSION: *C. ruelensis* shows a similarity to the *C. haimeana* group, but the ornamentation is quite distinct and unlike any of these in detail. The puncta between the ridges are unlike any other inter-costal ornamentation developed in this group.

One specimen of a related form has been found in a sample from Moiselles (Pl. 7, fig. 11). The ridges form the same pattern as in *C. ruelensis* but they are all of about equal prominence. This is *Cytheretta* sp.A.

Cytheretta eocaenica Keij

(Pl. 1, fig. 2; Pl. 7, figs 1–10)

1852 *Cythere jurinei* (non. von Munster); Bosquet: 56 (pars), pl. 2, fig. 9.
1955 *Cytheretta jurinei* (non. von Munster); Apostolescu: 263, pl. 5, figs 86–89; pl. 6, figs 90–91.
1957 *Cytheretta eocaenica* Keij: 134, pl. 6, fig. 6; pl. 10, figs 2–4.

DIAGNOSIS: (After Keij, 1957): 'A species of the genus *Cytheretta* with the following characteristics; anterior margin obliquely rounded, obtusely angular ventrally; with horizontal rows of rounded depressions posteriorly; inner margin with three inward protrustions in the ventral half of the valve.'

MATERIAL: 109 valves and carapaces from the Sables de Lède of Bambrugge were available for study, donated by Dom. R. Rome, together with nine valves and carapaces from the Lutetian IV of Damery. Io 3839–44.

TYPE LOCALITY AND HORIZON: Grignon; Lutetian IV.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Cuisian and Lutetian of the Paris Basin; Lutetian and Ledian of Belgium; Upper Bracklesham Beds of England.

DISCUSSION: Keij describes the ornamentation as consisting of 3–5 horizontal rows of rounded depressions in the postero-ventral part of the valve with additional widely scattered depressions in the female. The specimens from Bambrugge have some nine rows of pits in the postero-ventral region and some five in the antero-ventral region. There is a smooth area near the centre of the valve representing the sub-central plexus from which run two prominent rows of pits towards the direction of the anteroventral angle. The Damery specimens fit Keij's description with five postero-ventral rows of pits; the more ventrally placed pits, as developed at Bambrugge, are absent. However, the two prominent anterior rows can also be distinguished.

Another feature of the Bambrugge sample is the presence of a few very large individuals, about 1 in 8. These are similar in shape and ornamentation to the smaller specimens. The smaller individuals are definitely adults: the hinge, sexual dimorphism, thick shell and inner margin are all well developed. This is probably an example of post-maturation moulting.

DIMENSIONS:

	L	H	W	L/H
Female (normal)	0·78	0·47	0·40	1·66
Female (large)	0·93	0·59	0·49	1·58

Sex ratio: 1 : 3.

Cytheretta oligocaenica sp. nov.

(Pl. 8, figs 1–13)

DERIVATION OF NAME: From Oligocene; refers to the strata in which it is found.

DIAGNOSIS: A species of *Cytheretta* with an obliquely rounded anterior margin and slightly convex ventral margin in the left valve; ornamentation consists of up to 8 rows of pits in the postero-ventral region; there is often an ill-defined sulcus in the postero-lateral position.

HOLOTYPE: Io 3845, a female left valve.

PARATYPES: Io 3846–9.

MATERIAL: Couches du Phare (Biarritz), 55 valves and carapaces; Couches de l'Atalaye (Biarritz), 11 valves and carapaces; St. Geours de Maremne, 9 valves and carapaces; Blaignan, 5 carapaces.

TYPE LOCALITY AND HORIZON: Biarritz; Couches du Phare (RO 271); Stampian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Couches de l'Atalaye and Couches du Phare, Biarritz; Faluns Bleues of St. Geours de Maremne; Argile à algues, Blaignan.

DESCRIPTION: Sexual dimorphism is distinct. Sex ratio, 1 : 3. The left valve has a prominent posterior hinge-ear and a convex dorsal margin; the anterior margin is obliquely rounded; the ventral margin is slightly convex; the posterior margin is obliquely rounded. The greatest height is just to the anterior of centre. The right valve has its greatest height about one quarter of the way from the posterior margin and this results in a slight triangular shape as the almost straight dorsal margin slopes towards the anterior margin; the ventral margin is concave.

The ornamentation consists of up to 8 rows of pits in the postero-ventral region. An ill-defined sulcus is often present in the postero-lateral position.

The antero-dorsal lobe of the hinge of the left valve is swollen; the antero-ventral lobe is large and prominent; the antero-median tooth is large; the postero-median swelling is prominent. The anterior tooth of the right valve is crescentic-shaped in lateral view; in dorsal view both teeth of the right valve are large and squat (Plate 8, Fig. 8–13).

The inner margin has a narrow anterior indentation and small ventral and posterior indentations; the anterior segment is semi-circular; the median segment is long with a gentle upward slope; the posterior segment is short and semi-circular. There are some 35 anterior and 17 ventral radial pore canals. The posterior radial pore canals are very closely packed and there are about 80 of them; they are not divisible into two groups. The selvage is very close to the anterior margin; there is a small posterior flange groove and a larger ventral one; a weak list is present.

As with *C. eocaenica*, there are a few very large individuals, about 10 %.

DIMENSIONS:

	L	H	W	L/H
Female	0·85	0·53	0·51	1·60
Male	0·86	0·49	0·41	1·71
Large form, male	0·98	0·58	—	1·70

DISCUSSION: This is very similar to *C. eocaenica* Keij. It differs in shape; the antero-ventral angle is rounded and not angular as in *C. eocaenica*, the ventral margin is slightly convex, not straight, and the greatest height is just to the anterior of centre, whereas it is about one third of the way from the anterior in *C. eocaenica*. The right valve is much higher in the posterior in *C. oligocaenica*. There are more anterior radial pore canals in the latter, 35 compared with 27–30. The inner margin is similar in both species, and in this respect they differ from *C. jurinei* (von Munster), which has a very large and circular posterior indentation.

See also *C. geoursensis* sp. nov.

Cytheretta geoursensis sp. nov.

(Pl. 10, figs 1, 3, 5)

DERIVATION OF NAME: From St. Geours de Maremne.

DIAGNOSIS: A large species of *Cytheretta* with a prominent posterior hinge ear, convex ventral margin of left valve, and a finely punctate outer surface.

HOLOTYPE: Io 3850, a female left valve.

PARATYPES: Io 3851–2.

MATERIAL: Eight valves and carapaces.

TYPE LOCALITY AND HORIZON: Marnière d'Escornbéou, near St. Geours de Maremne (Aquitaine Basin); Faluns bleues, Oligocene(?) (Chattian?).

STRATIGRAPHICAL RANGE AND DISTRIBUTION: So far only known from the type locality.

DESCRIPTION: Sexual dimorphism is distinct; sex ratio, 1 : 3. The left valve has a very prominent posterior hinge ear; the dorsal margin is strongly convex; the anterior margin is obliquely rounded; the ventral margin is strongly convex, particularly towards the posterior; the posterior margin is obliquely rounded. The right valve has a slightly convex dorsal margin and a slightly concave ventral margin.

The whole outer surface of the carapace is covered with a very superficial appearing punctation. Two or three rows of pits in the postero-lateral position can be seen on some specimens, and one right valve has these quite prominently developed.

The hinge, inner margin, selvage and list are as for *C. oligocaenica*. There are 27 anterior radial pore canals, but the exact number of posterior radial pore canals could not be determined.

DIMENSIONS:

	L	H	W	L/H
Female	0·98	0·58	0·60	1·69
Male	1·07	0·58	0·50	1·84

DISCUSSION: This could perhaps be regarded as a post-maturation moult stage of *C. oligocaenica* sp. nov. similar to those already described. However, unlike these, this is not merely a larger version of the small forms. It differs from *C. oligocaenica* in shape, particularly the strongly convex ventral margin of the left valve; in ornamentation; and in the number of anterior radial pore canals (27 compared with 35).

Cytheretta carita sp. nov.

(Pl. 9, figs 5, 8, 9–11; Pl. 10, fig. 7. Text-fig. 14)

DERIVATION OF NAME: Latin—carita, to be without or to be deprived; refers to the lack of ornamentation.

DIAGNOSIS: A smooth species of *Cytheretta* with an obliquely rounded anterior margin and two 'dimples' in the posterior.

HOLOTYPE: Io 3853, a female left valve.

PARATYPES: Io 3854–8.

MATERIAL: 39 valves and carapaces from the type Auversian; 57 from Moiselles; 5 from Le Ruel, Sables de Cresnes; 1 from the Marnes à *P. ludensis* at Verzy.

TYPE LOCALITY AND HORIZON: Carriere de Moiselles; Sables de Beauchamp.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: 'Bartonian' of the Paris Basin.

DESCRIPTION: Sexual dimorphism distinct; sex ratio, 1 : 2·5. The dorsal margin of the left valve has a prominent posterior hinge ear, is straight until about the mid-point when it slopes down to the anterior margin, which is very obliquely rounded. The ventral margin is slightly convex and curves into the posterior margin, which is rounded. The dorsal margin of the right valve is more irregular; a slight hinge ear is present at the posterior and the anterior tooth projects beyond the margin. There is a marked concavity between the hinge ear and the posterior margin. The ventral margin is slightly concave. In dorsal view it is ovate.

The valve is smooth. At the posterior are two dimples, one in the postero-ventral angle and the other higher along the posterior margin.

In the hinge of the left valve, the antero-ventral lobe is weakly developed, leaving the anterior socket almost open ventrally; the antero-dorsal lobe is flat to lobate and small; the antero-median tooth is large; the postero-median swelling small. In the right valve the anterior tooth is large and the posterior tooth is slightly reniform.

The anterior indentation of the inner margin is narrow; the ventral deep and prominent; and the posterior broad, but deep. The median segment is almost flat; the posterior segment is steeper, but not very pronounced. The muscle scars are normal, the two ventral scars being close together. They are situated in a slight pit.

The selvage runs along the anterior margin of both valves, so there is no anterior flange groove. A ventral flange groove is well developed, as well as a small posterior one. A very weak list is present along the ventral and posterior duplicature.

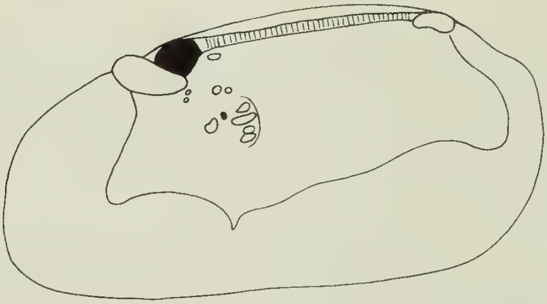

FIG. 14. *Cytheretta carita* sp. nov.; female right valve; ×75.

DIMENSIONS:

	L	H	W	L/H
Female	0·87	0·55	0·43	1·58
Male	0·93	0·53	0·41	1·75

DISCUSSION: This differs from other smooth *Cytheretta* species such as *C. rhenana* Triebel by its shape and the presence of the posterior dimples. It shows a very close relationship to *C. eocaenica*, but lacks the longitudinal rows of pits of the latter.

Cytheretta cellulosa sp. nov.

(Pl. 9, figs 1–4, 6, 7)

DERIVATION OF NAME: Latin—cellulosus, full of little cells, referring to the ornamentation.

DIAGNOSIS: A species of *Cytheretta* with 13 rows of pits which converge at the posterior; dorsal area is smooth.

HOLOTYPE: Io 3859, a female left valve.

PARATYPES: Io 3860–63.

MATERIAL: Eight valves and carapaces from the type Auversian; fourteen valves and carapaces from Moiselles.

Type locality and horizon: Auvers-sur-Oise; Sables d'Auvers.

Stratigraphical range and distribution: Auversian of the Paris Basin.

Description: Sexual dimorphism is pronounced; sex ratio, 1 : 3. The dorsal margin of the left valve has a prominent posterior hinge ear and is convex. The anterior margin is slightly obliquely rounded; the ventral margin is straight in the central portion; the posterior margin is very obliquely rounded. In the male, the ventral margin has a very straight appearance. The right valve has a concave ventral margin. Carapace is ovate in dorsal view.

The ornamentation of the left valve consists of 13 rows of small pits. In the posterior region these rows converge and merge into one another; the pitting is very fine. In the central region the rows are distinct and consist of a single line of pits larger in the centro-dorsal region. The central rows converge upon an ill-defined sub-central plexus, which is almost smooth. To the anterior of this the rows consist of double rows of puncta; there are five of these, together with three ventral rows of single puncta which are continuous along the ventral region. The dorsal area is smooth. The right valve is similar except that there are single rows of pits in the anterior region.

The hinge of the left valve has a swollen antero-dorsal lobe; a small antero-ventral lobe so that the anterior socket is virtually open ventrally, as is the posterior socket; a large antero-median tooth; and a small inconspicuous postero-median swelling. The anterior tooth of the right valve is large, and the posterior tooth is prominent.

The inner margin could not be clearly seen. There are some 20 anterior radial pore canals. The central muscle scars are in a slight pit, and the two ventral ones are close together. One very prominent dorsal muscle scar can be seen above the fulcral point. The selvage runs close to the anterior margin; there is a ventral flange groove and a small posterior one. A weak list is present along the anterior, ventral and posterior parts of the duplicature.

Dimensions:

	L	H	W	L/H
Female	0·80	0·49	0·38	1·65
Male	0·93	0·51	0·43	1·82

Discussion: *C. cellulosa* bears a ressemblance to *C. tenuipunctata* (Bosquet), but the pattern of pits is different and the outline of the valve is completely different. *C. eocaenica* Keij from the Ledian of Bambrugge often develops pits over a large area, although never to the same extent as here. The shape, however, is similar, and it is thought likely that *C. eocaenica* is the ancestor of *C. cellulosa*, with such forms as those from Bambrugge as intermediates.

Cytheretta* aff. *cellulosa

1968 *Cytheretta minor* (non Lienenklaus) Haskins: 167, pl. 1, figs 30–35.

Discussion: Haskins records this from the Barton Beds in Alum Bay. In many respects it appears to be intermediary between *C. cellulosa* and *C. minor*.

Superspecies ***Cytheretta laticosta*** (Reuss)

Diagnosis: A group of species of the genus *Cytheretta* characterized by three longitudinal ridges. The dorsal ridge is convolute; the median ridge contains four depressions along its ventral side; the ventral ridge is the most prominent of a group of ridges developed in the ventral part of the valve.

Description: The carapace generally has a massive appearance with a thick shell; it is strongly inequivalve, and sexual dimorphism is pronounced. In the left valve there is a prominent posterior hinge ear. In the right valve the anterior tooth projects beyond the margin and the ventral margin is concave. In dorsal view the carapace is swollen posteriorly in both males and females, but this is more pronounced in the latter.

The ornamentation consists predominantly of three thick longitudinal ridges. The dorsal ridge runs along the margin, but does not reach the anterior margin; the median ridge swells in the central region and contains four depressions on its ventral side, each of which has a normal pore canal opening into it. This runs from the anterior margin to the posterior, where it curves upwards to form a margin to the hinge ear. The ventral ridge also contains four depressions with normal pore canals, much better seen in the right valve. In the left valve this ridge is really the most pronounced of a series of ventral ridges, of which there are seven in all. In the right valve the lower ventral ridges are indistinct or absent, and this gives the whole valve a strongly tri-costate appearance. A prominent marginal rim runs around the anterior margin and the anterior portion of the ventral margin. In the right valve there is a posterior marginal rim. There are some eight marginal antero-ventral denticles, each of which bears a radial pore canal, and three posterior ones. The latter are larger in the right valve. The whole surface is finely punctate, although this can only be seen on well preserved specimens.

The hinge of the left valve has a swollen, knob-like, antero-dorsal lobe; the antero-ventral lobe is small; the antero-median tooth is prominent; postero-median swelling is small. In the right valve the anterior tooth is large and the posterior tooth circular in plan.

The selvage is prominent, particularly in the right valve; there is a well developed flange groove in the anterior, ventral, and posterior; and a list is present in the postero-ventral region. There are some 32 anterior radial pore canals, 20 ventral, and 18 posterior; and 29 normal pore canals which are arranged in sympathy with the ornamentation (Text Fig. 15). The central and dorsal muscle scars are as for the genus.

Cytheretta laticosta (Reuss)

(Pl. 1, fig. 3; Pl. 10, figs 2, 4, 6, 8, 9; Pl. 12, figs 1–2 5; Text-fig. 15).

1850 *Cypridina laticosta* Reuss: 87, pl. 11, fig. 13.
1857 *Cythere plicata* var. *laticosta* (Reuss); Jones: 32, pl. 5, fig. 8 (pars).
1889 *Cythere plicta* var. *laticosta* (Reuss); Jones and Sherborn: 29 (pars).
1957 *Cytheretta laticosta* (Reuss); Keij: 137, pl. 18, figs 15–18; pl. 21, fig. 16.
1968 *Cytheretta laticosta* (Reuss); Haskins: 166 (pars), pl. 2, figs 23, 27, 28.

Diagnosis: A member of the superspecies *C. laticosta* with an evenly rounded anterior margin, convolute dorsal ridge and small areas of coarse puncta around the median and ventral ridges.

Material: Three carapaces from the Lower Barton Beds of Alum Bay; numerous specimens from the Middle and Upper Barton Beds of Barton, and Alum Bay; fifteen valves and carapaces from the Marnes à *P. ludensis* of Verzy, and five from Chavençon. Io 3864–70.

Type locality and horizon: Barton Clay of Barton (see discussion).

Stratigraphical range and distribution: Barton Clay of Barton, Alum Bay and Whitecliff Bay; Marnes à *P. ludensis* of Verzy and Chavençon; Argile d'Asche of Oedelem (Belgium).

Description: Sex ratio, 1 : 1·6. The carapace is massive, the shell is thick. The dorsal ridge is thick with convolutions forming some six depressions, which bear normal pore canals. The median ridge has a prominent swelling in the central part and has an area of coarse puncta around the four depressions. The ventral ridge likewise has an area of coarse puncta.

The inner margin has a narrow and deep anterior indentation, particularly in the right valve, and a prominent ventral one. The anterior segment is sharply rounded. The median and posterior segments are inseparable; they slope up to the posterior indentation, which is quite close to the ventral margin.

Dimensions:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·80 ± 0·02	0·50 ± 0·01	1·60 ± 0·04	0·46	0·79	0·42	1·88
Male	0·86 ± 0·02	0·49 ± 0·01	1·76 ± 0·04	0·45	0·89	0·46	1·94

Discussion: Reuss described this as coming from the London Clay of Barton, Hampshire. This relates to the idea prevalent in the early 19th century that the clay at Barton was of the same age as that at London; in fact, the London Clay is Lower Eocene, while the Barton Clay is Upper Eocene.

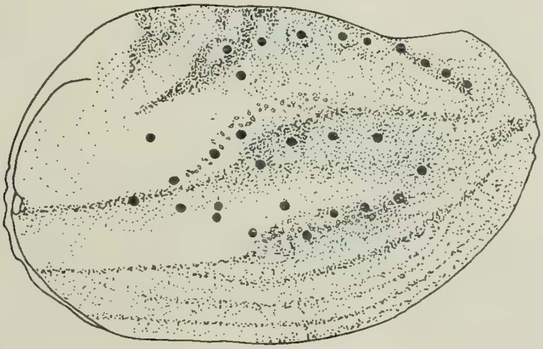

Fig. 15. *Cytheretta laticosta* (Reuss) showing distribution of normal pore canals in relationship to ornamentation; ×75.

Cytheretta forticosta sp. nov.

(Pl. 11, figs 1–4, 8, 9; Pl. 12, figs 6–12)

1857 *Cythere plicata* (non. von Munster); Jones: 32 (pars).
1968 *Cytheretta laticosta* (Reuss); Haskins: 166 (pars), pl. 2, figs 19–22, 24–26, 29.

Derivation of name: Latin—fortis, strong; costa, ridge. Refers to the three strong longitudinal ridges.

Diagnosis: A member of the superspecies *C. laticosta* with an obliquely rounded anterior margin and simple median ridge.

Holotype: Io 3871, a female left valve.

Paratypes: Io 3872–8.

Material: Numerous specimens from the localities mentioned below.

Type locality and horizon: Fisher Beds 17–18, Upper Bracklesham Beds, Whitecliff Bay.

Stratigraphical range and distribution: Upper Bracklesham Beds of Whitecliff Bay, Selsey Bill, and Bramshaw (New Forest); Sables de Cresnes, Le Ruel.

Description: Sex ratio, 1 : 2·5. The carapace is massive. The left valve of the female has a circular outline; the dorsal margin is strongly convex; the anterior margin is obliquely rounded; the ventral margin is short and straight; the posterior margin is very obliquely rounded. In the right valve the dorsal outline is irregular, and the ventral margin is concave.

The dorsal ridge has five depressions, each of which bears a normal pore canal. The four pits on the median ridge are simple; those on the ventral ridge are prominent in both valves. The surface of the valve is punctate. In the right valve the ventral group of ridges are distinct in the anterior and posterior regions.

The inner margin is similar to that of *C. laticosta* except that the joint median and posterior segments have two undulations.

Dimensions:

	Left valve			Right valve			
	L	H	L/H	W	L	H	L/H
Female	0·77 ± 0·03	0·52 ± 0·02	1·46 ± 0·04	0·52	0·83	0·45	1·84
Male	0·87 ± 0·03	0·54 ± 0·02	1·62 ± 0·05	0·52	0·90	0·48	1·88

Cytheretta porosacosta sp. nov.

(Pl. 11, figs 5–7; Pl. 12, figs 3, 4)

1857 *Cythere plicata* (non. von. Munster); Jones: 32 (pars), pl. 4, fig. 16; pl. 5, fig. 8.
1889 *Cythere plicata* (non. von Munster); Jones and Sherborn: 29 (pars), pl. 1, fig. 18.
1968 *Cytheretta laticosta* (Reuss); Haskins: p. 166 (pars).

Derivation of name: Latin—porosus, full of holes; costa, ridge. Refers to the heavily punctate ornamentation.

Diagnosis: A member of the superspecies *C. laticosta* with an evenly rounded anterior margin, simple ridge, and wide areas of large puncta.

Holotype: Io 3879, a female left valve.

Paratypes: Io 3880–83.

Material: Numerous valves from the localities mentioned below.

Type locality and horizon: Colwell Bay, Isle of Wight; Middle Headon Venus Bed.

Stratigraphical range and distribution: Brockenhurst Beds of Brockenhurst and Whitecliff Bay; Middle Headon Beds of Colwell Bay, Headon Hill, Whitecliff Bay, Milford, and Brockenhurst.

Description: The dorsal margin of the left valve is slightly irregular due to the over-reach of the dorsal ridge; otherwise it is straight to slightly convex. The anterior margin is evenly rounded; the ventral margin is slightly concave; and the posterior margin obliquely rounded.

In the left valve the dorsal ridge has several faint depressions, but is fairly simple. The median ridge is narrow, with four very faint depressions on the ventral side. There is no strong ventral ridge. In the right valve however, the ventral ridge is distinct due to the absence of the lower ventral ridges. Large areas of coarse puncta are developed amongst the ventral group of ridges and around the median ridge.

Dimensions:

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·74±0·02	0·44±0·01	1·68±0·025	0·74	0·38	1·92
Male	0·78±0·02	0·42±0·01	1·84±0·04	0·82	0·40	2·05

Discussion: The three species described are only part of the superspecies *C. laticosta*. Other forms not studied are found in the London Clay of the London and Hampshire basins and the Lower and Middle Bracklesham Beds.

The most noticeable difference between these species is the shape of the carapace. This is most marked in the female dimorph. The species represent three quite distinct groups (Text-fig. 16). The L/H ratio is:

	Female	Male
C. forticosta	1·46±0·04	1·62±0·05
C. laticosta	1·60±0·03	1·76±0·04
C. porosacosta	1·68±0·025	1·84±0·04

The anterior margin changes from obliquely rounded in *C. forticosta* to evenly rounded in *C. laticosta* and *C. porosacosta*.

The three longitudinal ridges are more complex in *C. laticosta*. The dorsal ridge is convolute and complicated. The four depressions in the median ridge are prominent and punctate; in *C. forticosta* there are only four large puncta and no depressions; in *C. porosacosta* the depressions are almost absent. The ventral ridge has a prominent central area with coarse puncta; these are not present in *C. forticosta*, while in *C. porosacosta* the puncta cover a large area of the valve. In the right valve of *C. forticosta* the ventral group of ridges are stronger than in *C. laticosta* and *C. porosacosta*.

The trends seen in these three species are, therefore:
(i) Change from a rounded to a more elongate shape.
(ii) Anterior margin from obliquely rounded to evenly rounded.
(iii) Development of coarse puncta, especially around the median and ventral ridges.

The group of specimens from Le Ruel have a mean L/H ratio of 1·43 and have a more rounded appearance than the English *C. forticosta*. The specimens from Selsey Bill and Bramshaw are more elongate, with a mean ratio of 1·50. The Whitecliff

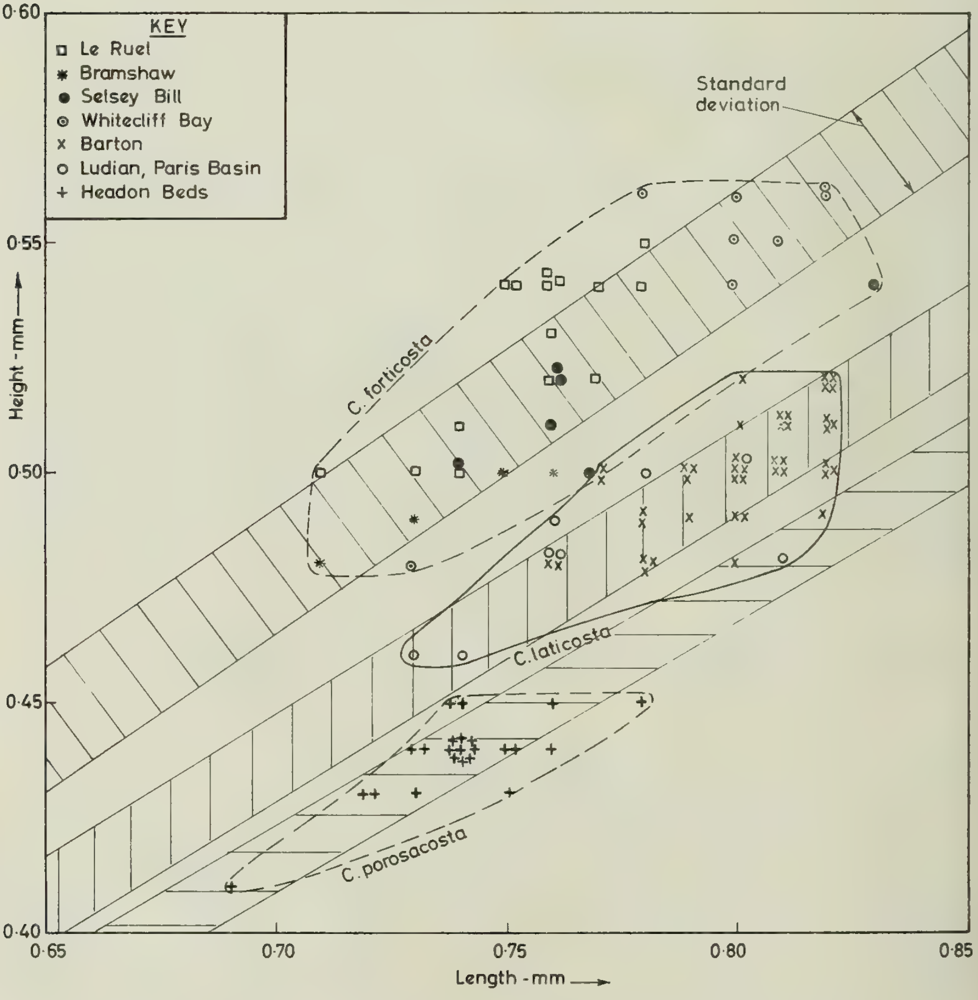

FIG. 16. Size distribution of species of the superspecies *C. laticosta* (Ruess).

Bay specimens have a mean of 1·46 and have an even distribution. There is considerable overlap between these specimens, however, which does not occur between these specimens of *C. laticosta* and *C. porosacosta.*

The variation in size is most noticeable between *C. porosacosta* on the one hand and *C. laticosta* and *C. forticosta* on the other. This is thought to be environmental because *C. porosacosta* is found in beds with a mixed marine and brackish water fauna. The thinner shell of *C. porosacosta* and the general weakness of the three ridges is probably also connected with this. The specimens of *C. forticosta* from Bramshaw and Selsey are seen to be smaller than those from Whitecliff Bay; and *C. laticosta* from the Ludian of the Paris Basin are smaller than those from the Barton Clay. This may be environmental. The specimens from Le Ruel show a large range in size, due perhaps to the nature of the Sables de Cresnes, which are coarse-grained current-bedded sands, often with rolled macro-fossils.

Eventually, specimens of an intermediate nature may be found between these three species, in which case they will become subspecies. It is thought highly likely that such intermediates exist, but at the moment there are present three distinct groups with no overlap.

Superspecies ***Cytheretta tenuipunctata*** (Bosquet)

The superspecies *C. tenuipunctata* comprises a group of ostracods with similarities in shape of lateral view, ornamentation, and internal structures. The following species and subspecies are included:

C. tenuipunctata tenuipunctata (Bosquet)
C. tenuipunctata absoluta subsp. nov.
C. tenuipunctata lirata subsp. nov.
C. tenuistriata tenuistriata (Reuss)
C. tenuistriata ornata subsp. nov.
C. bernensis Oertli
C. buttensis sp. nov. *buttensis* subsp. nov.
C. buttensis reticulata subsp. nov.
C. minipunctata sp. nov.

The following are tentatively included:

C. triebeli Oertli
C. variabilis Oertli
C. ramosa ramosa (Lienenklaus)
C. ramosa sublaevis Triebel

There are further groups of ostracods from the Oligocene of western Europe which are also closely related to the superspecies. These are discussed below.

DIAGNOSIS: A superspecies of the genus *Cytheretta* with up to 13 longitudinal ridges, often stronger in the ventral half of the valve, which form a regular pattern, although differing slightly in detail between species. There are three ridges in the anterior part which run from the region of the sub-central plexus towards the antero-ventral angle. In lateral view the carapace is elongate with pronounced sexual dimorphism;

in dorsal view it is ovate or tapered towards the anterior. The valves are not strongly inequivalve.

Description: The shape varies, but in general it is elongate in lateral view. In dorsal view it is usually ovate, or slightly triangular with its apex at the anterior. Sexual dimorphism is pronounced; sex ratio, 1 : 2. The valves are inequivalve, but not strongly so.

Up to 13 longitudinal ridges are developed, which may be strong or weak. In some species no ridges are present in the dorsal half of the valve. The ornamentation between the ridges varies from species to species. A complete development is seen in Text-fig. 17.

Ridge no. 1 runs from near the posterior hinge ear, disappearing to the anterior of the sub-central plexus. No. 2 is often formed of a series of short curved ridges, usually broken and bifurcating. No. 3 joins no. 2 in the posterior, runs above the sub-central plexus, and just to the anterior of it joins no. a. In some species, and particularly in the right valve, ridge a is very prominent, sloping sharply towards the antero-ventral angle. The sub-central plexus is an irregular, smooth area, varying from species to species, but usually prominent. Three parallel ridges, a, b, and c, run from the sub-central plexus towards the antero-ventral angle; these are diagnostic of the superspecies. There are another three parallel ridges, 4, 5, and 6 to the posterior of the sub-central plexus. Ridge no. 7 joins no. 4 at the posterior and no. 8 at the anterior. Ridges 8–13 are approximately parallel to the ventral margin. The ridges form a complicated pattern at the posterior, seen in Text-fig. 17. Ridges 9–13 disappear amongst fine puncta at the posterior.

The antero-dorsal lobe of the hinge of the left valve is prominent and slightly swollen; the antero-ventral lobe is prominent; the antero-median tooth is well developed, but the postero-median swelling is virtually absent. In the right valve the anterior tooth is slightly reniform in shape; in dorsal view the two teeth appear to be almost equal in size.

The selvage is prominent along the ventral and posterior margins. A wide flange groove with a well marked flange is present in the ventral region; in the posterior the flange groove is narrow and a small fringe is developed. Along the anterior

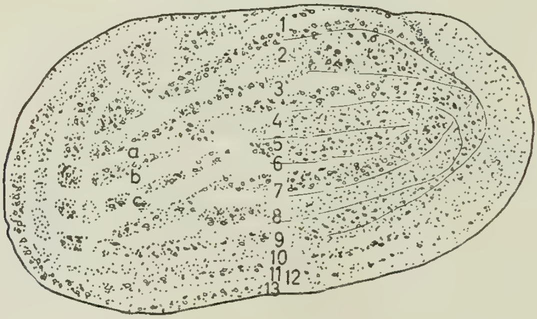

Fig. 17. Ridges of the superspecies *Cytheretta tenuipunctata* (Bosquet). The specimen is *C. tenuistriata ornata* subsp. nov; ×75.

margin a few very small denticles are present; a radial pore canal opens from each of them. There are some 35 anterior radial pore canals and some 40 closely spaced posterior pore canals. The inner margin varies slightly from species to species.

Cytheretta tenuipunctata (Bosquet)

Diagnosis: A species of the superspecies *C. tenuipunctata* with a prominent sub-central plexus and a medium to coarse pitting between the ridges, the pits often being in double rows in the median part of the valve. The ridges are strongly developed.

Discussion: This was described by Bosquet from the Argile à *N. comta* of Belgium. It is very similar to *C. tenuistriata* (Reuss), and Keij (1957) believed that the two were synonymous. This was because of the similarities in ornamentation. The two species are here regarded as distinct, but are placed within the same superspecies. *C. tenuistriata* is a much larger ostracod than *C. tenuipunctata*, but in itself this need not be important. In the Paris Basin however, the two co-exist without intermediaries, so that the difference in size is very obvious; thus they formed two separate populations which must be assumed to be specifically distinct. The ornamentation between the ridges consists of a coarser pitting in *C. tenuipunctata* than in *C. tenuistriata*.

Cytheretta tenuipunctata tenuipunctata (Bosquet)

1852 *Cythere jurinei* (non. von Munster); Bosquet: 56 (pars).
1852 *Cythere jurinei* var. *tenuipunctata* Bosquet: 56, pl. 2, fig. 10.
1957 *Cytheretta tenuipunctata* (Bosquet); Keij: 138, pl. 5, fig. 21; pl. 6, fig. 5.

Type locality and horizon: Berg, near-Kleine Spouwen, Belgium; Argile à *N. comta* (Rupelian).

Stratigraphical range and distribution: Upper Tongrian (?) and Lower Rupelian of Belgium.

Dimensions: (After Keij):

Lectotype (Male R)	0·96 × 0·47
Female L	0·88 × 0·51

Discussion: Keij (1957) has selected a lectotype and redescribed species as having 6–8 ridges which gradually vanish towards the anterior and posterior margins; between the ridges are fine pits, mostly in two rows; towards the dorsal margin the surface is pitted, but without ridges; the areas along the anterior, posterior, and dorsal margins are smooth; and a sub-central plexus is well developed.

C. tenuipunctata tenuipunctata differs from the two subspecies described below by the absence of the dorsal ridges.

Cytheretta tenuipunctata absoluta subsp. nov.

Pl. 14, figs 1–4, 6, 7; Text-fig. 18)

DERIVATION OF NAME: Latin—absolutus, complete; refers to the ornamentation which completely covers the valve, unlike *C. tenuipunctata tenuipunctata*.

DIAGNOSIS: A subspecies of *C. tenuipunctata* in which the full 13 ridges of the superspecies *C. tenuipunctata* are developed; the ornamentation between the ridges consists of a fine pitting, in double rows in the median and dorsal parts of the valve, and single rows between the ventral ridges.

HOLOTYPE: Io 3884, a female left valve.

PARATYPES: Io 3885–9.

MATERIAL: 55 adult valves and carapaces and 68 larval stages from Cormeilles.

TYPE LOCALITY AND HORIZON: Cormeilles-en-Parisis; Marnes à Huîtres.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Marnes à Huîtres of the Paris Basin.

DESCRIPTION: The dorsal and ventral margins of the valves are sub-parallel, particularly in the left valve. In the latter there is a prominent posterior hinge ear; the dorsal margin is slightly convex; the anterior margin is evenly rounded; the ventral margin is straight or slightly concave; the posterior margin obliquely rounded In the right valve the ventral margin is concave and there is a concavity in the postero-dorsal position. In dorsal view the carapace is ovate.

The ridges are well defined, particularly in the right valve. The ornamentation between the ridges consists of a fine pitting. Between ridges 1, 2, 3 and 4, 6 and 7, a, b, c, there is a double row of pits; between the ventral ridges there is a single row. The anterior region is reticulate.

The inner margin (Text-fig. 18) has a broad anterior and posterior indentation and a well marked ventral indentation. The anterior segment is rounded, and the joint median and posterior segments are undulating.

Two larval stages have been recognised (Text-fig. 19). In these the complete ridge pattern of the adult is developed with small puncta between them; these are in rows of three between ridges no. 6 and 7, and in double rows between the others. Ridges 8 and 9 are very strong in the posterior region and in larval stage 7 there is a distinct swelling in this region.

DIMENSIONS:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·87 ± 0·03	0·49 ± 0·01	1·76 ± 0·05	0·43	0·87	0·46	1·89
Male	1·00 ± 0·02	0·51 ± 0·01	1·96 ± 0·02	0·43	0·98	0·50	1·96

DISCUSSION: This subspecies differs from *C. tenuipunctata tenuipunctata* in the larger number of ridges, caused by their presence in the dorsal regions. It differs from *C. tenuipunctata lirata* subsp. nov. in having a slightly different shaped dorsal margin, the latter having a weak anterior hinge ear in the left valve, and in the ornamentation between the ridges which show a great deal of variation in *C. tenuipunctata lirata*.

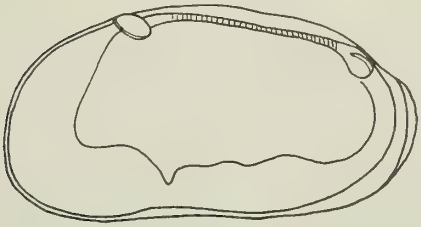

FIG. 18. *Cytheretta tenuipunctata* (Bosquet) *absoluta* subsp. nov.; female right valve; ×75.

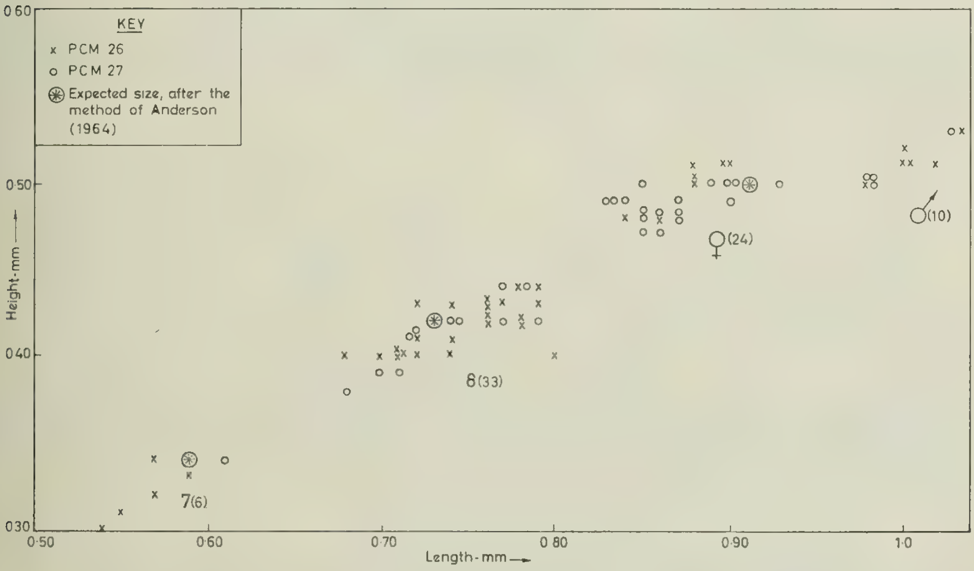

FIG. 19. Size distribution of the adults and larval stages of *Cytheretta tenuipunctata* (Bosquet) *absoluta* subsp. nov.

Cytheretta tenuipunctata lirata subsp. nov.

(Pl. 14, figs 5, 8–10; Pl. 15, fig. 10; Pl. 16, fig. 4)

1895 *Cythere jurinei* (non. von Munster); Lienenklaus: 8 (pars).

DERIVATION OF NAME: Latin—lirata, earth or ridge formed by ploughing; refers to the ornamentation.

DIAGNOSIS: A subspecies of *C. tenuipunctata* in which the full 13 ridges of the superspecies *C. tenuipunctata* are developed; the ornamentation between the ridges varies from pitting to reticulation; a weak hinge ear is developed in the left valve.

HOLOTYPE: Io 3890, a female left valve.

PARATYPES: Io 3891–95.

MATERIAL: 37 valves from Auvers-St-George.

Type locality and horizon: Auvers-St-George; Stampian.

Stratigraphical range and distribution: Stampian of the Paris Basin.

Description: The shape of the dorsal margin of the left valve is convex with two slight concavities to the anterior and posterior of the posterior and anterior hinge ears respectively. Otherwise the shape is similar to *C. tenuipunctata absoluta.* The 13 ridges are developed, although a few specimens show a smooth area in the antero-dorsal region, but this is small. Ornamentation between the ridges shows a large amount of variation; pits are usually developed, sometimes in a double row, but more often in a single row; in other specimens a fine reticulation is present, and in others the longitudinal ridges are very strong with a relatively inconspicuous ornamentation between them. The sub-central plexus is well developed. There is an anterior area of reticulation. The inner margin is similar to that of *C. tenuipunctata absoluta.*

Dimensions:

	Left valve			Right valve			
	L	H	L/H	½W	L	H	L/H
Female	0·89±0·03	0·49±0·01	1·82±0·03	0·29	0·90	0·45	2·00
Male	0·96	0·49	1·97	0·29	0·98	0·48	2·04

Discussion: See *C. tenuipunctata absoluta* subsp. nov.

Cytheretta tenuistriata (Reuss)

Diagnosis: A species of the superspecies *C. tenuipunctata* of large size, with well developed sub-central plexus and distinct ornamentation between the ridges.

Cytheretta tenuistriata tenuistriata (Reuss)

(Pl. 16, figs 5, 7)

1853 *Cytherella tenuistriata* Reuss: 676, pl. 9, fig. 10.
1905 *Cythereis jurinei* (non. von Munster); Lienenklaus: 31 (pars).
1952 *Cytheretta tenuistriata* (Reuss); Triebel: 22, pl. 3, fig. 12–15.
1956 *Cytheretta tenuistriata* (Reuss); Oertli: 61, pl. 6, fig. 163–165.

Material: Specimens from several localities around Weinheim; Io 3896–7.

Type locality and horizon: Weinheim, Mainz Basin; Unterer Meeressand.

Stratigraphical range and distribution: Unterer Meeressand of the Mainz Basin, Blaue Ton of Switzerland; Rupelian.

Diagnosis and description: The male has an anterior hinge ear in the left valve which, together with the posterior hinge ear, gives the dorsal margin an undulating appearance with two concavities. The anterior hinge ear is not present in the female, so the dorsal margin of the left valve is regular, and the valve has its greatest height close to the anterior end. The ornamentation is not strong; the ridges are weakly defined and in between them are double rows of small pits. The anterior and posterior areas are smooth.

DIMENSIONS (After Triebel):

L Female	1·08–1·13mm
Male	1·22–1·28mm

DISCUSSION: See *C. tenuistriata ornata* below.

Cytheretta tenuistriata ornata subsp. nov.

(Pl. 13, figs 1–12; Text-figs 17, 20)

1852 *Cythere jurinei* var. *tenuipunctata* Bosquet: 56 (pars).
1895 *Cythere jurinei* (non. von Munster); Lienenklaus: 8 (pars).

DERIVATION OF NAME: Latin—orno, ornamented; refers to the strong ornamentation.

DIAGNOSIS: A subspecies of *C. tenuistriata* with strong ornamentation.

HOLOTYPE: Io 3898, a female left valve.

PARATYPES: Io 4020–7.

MATERIAL: 32 valves from Auvers-St-George, 3 valves from Morigny; Io 3899.

TYPE LOCALITY AND HORIZON: Auvers-St.-George; Stampian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Stampian of Auvers-St.-George, Jeurre, and Morigny in the Paris Basin.

DESCRIPTION: The dorsal margin of the left valve of both the male and the female is almost straight with two slight concavities, one to the anterior of the posterior hinge ear and the other to the posterior of the weakly developed anterior hinge ear. The anterior margin is evenly rounded; the ventral margin is concave; and the posterior margin is obliquely rounded. In the right valve two concavities are present, one at the postero-dorsal angle and the other at the antero-dorsal angle.

The ridges are well developed and broad; there is a well marked anterior zone of reticulation. The ornamentation between the ridges consists of puncta arranged in three rows, or two rows between the ventral ridges. The sub-central plexus is large and prominent.

The inner margin has three broad indentations; the posterior segment has a greater slope than the median segment.

Three larval stages have been recognized, no. 6, 7, and 8. Ridges are weakly developed, being stronger in the right valve than in the left. In no. 8 all the ridges are present with a similar arrangement to those of the adult; there is a fine punctation between them. In no. 7 only the more ventral ridges are seen (ridges 4–13), and in no. 6 a few very faint lines can be seen in the postero-ventral region, where there is a slight swelling.

DIMENSIONS:

Length of combined left and right valves:

Female	1·05 ± 0·01
Male	1·15 ± 0·03

	Left valve				Right valve		
	L	H	L/H	½W	L	H	L/H
Female	1·03	0·58	1·78	0·31	1·02	0·51	2·00
Male	1·15	0·58	1·98	0·31	1·14	0·56	2·04

Mean length of larval stages:

No. 8, 0·88; no. 7, 0·74; no. 6, 0·61.

DISCUSSION: This differs from *C. tenuistriata tenuistriata* (Reuss) in the stronger ornamentation. The ridges are much more pronounced, there are no smooth area in the anterior and posterior regions, and the pitting between the ridges is finer than in *C. tenuistriata tenuistriata*. See also *C. tenuipunctata* and *C. minipunctata* sp. nov.

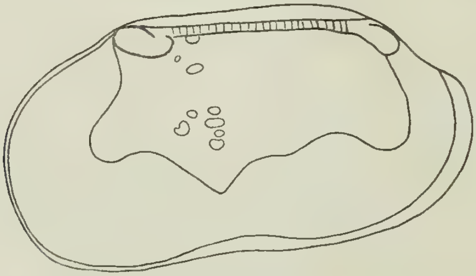

FIG. 20. *Cytheretta tenuistriata* (Reuss) *ornata* subsp. nov.; female right valve; ×75.

Cytheretta minipunctata sp. nov.

(Pl. 16, figs 1–3)

DERIVATION OF NAME: Latin—minus, small; punctata, small pits; refers to the ornamentation.

DIAGNOSIS: A species of the superspecies *C. tenuipunctata* with six faint ridges and a finely punctate ornamentation.

HOLOTYPE: Io 4028, a female left valve.

PARATYPE: Io 4029.

MATERIAL: 9 valves and carapaces from Cormeilles.

TYPE LOCALITY AND HORIZON: Cormeilles-en-Parisis; Bed no. 44 of Albissin, Couches de Sannois superieur.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Lower marine Sannoisian of the Paris Basin.

DESCRIPTION: The dorsal and ventral margins of the left valve are sub-parallel and almost straight; a posterior hinge ear is developed; the anterior margin is obliquely rounded towards ventral; the posterior margin is slightly pointed. In the right valve, the dorsal margin is convex and the ventral margin concave. In both valves there is an elongate dimple in the postero-ventral region.

Ornamentation consists of some 6 faint ridges which are developed in the ventral half of the valve, particularly in the median portion. In between the ridges are 2 or 3 rows of puncta; these also cover a large part of the dorsal area of the valve, where ridges are not developed.

Details of the interior are not clearly seen.

DIMENSIONS:

	L	H	L/H (Average)	W
Carapaces—Female	0·94–1·00	0·54–0·58	1·74	0·48
Male	1·10–1·15	0·58	1·93	0·50

DISCUSSION: This shows resemblances to *C. tenuistriata tenuistriata* in size and shape, but the ornamentation is completely different. The ornamentation is similar to that of *C. buttensis buttensis* subsp. nov, but has fewer ridges and is a different shape.

Cytheretta buttensis sp. nov.

DERIVATION OF NAME: French—butte, a hill; refers to the Butte de Cormeille and other buttes of the Paris region where the Sannoisian is found.

DIAGNOSIS: A species of the superspecies *C. tenuipunctata* showing great variation in the development of ridges and ornamentation. There are usually rows of small puncta between weak ridges; sometimes reticulate.

DESCRIPTION: The left valve has a posterior hinge ear, almost straight dorsal margin, evenly rounded anterior margin, straight ventral margin, and tapered posterior. The dorsal margin of the right valve is strongly convex, with its greatest height in about the centre. There is a dimple in the postero-ventral region of both valves. Ovate in dorsal view.

The inner margin (Text-fig. 21) is fairly regular; the posterior and anterior indentations are large, the anterior segment is flat, and the joint median and posterior segments have a gentle slope.

The larval stages are very triangular in shape with a pointed posterior end. The ornamentation is similar to that of the adults.

Three morphotypes have been recognized, which constitute two subspecies (Text-fig. 22).

Morphotype A:

This is characterized by the development of longitudinal ridges, usually stronger in the right valve. These follow the basic pattern of the superspecies; no. 7, with a sinuous course, joins no. 9 just before the anterior area of the reticulation; no. 8 joins no. 7 as a faint ridge. Between the ridges are parallel rows of small puncta; there are three rows between the ridges in the median and dorsal part of the valve and two in the ventral part. The sub-central plexus is only weakly developed.

Morphotype B:

Similar to Morphotype A except for the development of faint cross ridges between the longitudinal ones. The surface between the ridges is punctate, as in Morphotype A.

Morphotype C:

Strong cross ridges are developed between the longitudinal ones, which gives the valve a reticulate appearance. The surface between the ridges is smooth. The sub-central plexus is very weak. An additional ridge is present between no. 2 and 3.

Cytheretta buttensis buttensis subsp. nov.

(Pl. 15, fig. 10)

1960 *Cytheretta tenuistriata* Mehrotra (non Reuss) p. 80, pl. 1, figs 11–12.

Diagnosis and description: This consists entirely of Morphotype A.

Holotype: Io 4030.

Paratype: Io 4031.

Material: See fig. 22.

Type locality and horizon: Cormeilles-en-Parisis; Bed no. 46 of Mlle. Albissin, Couches de Sannois Supèrieur.

Stratigraphical range and distribution: Couches de Sannois supèrieur.

Dimensions (Carapace)

	L	H	L/H	W
Female	0·92 ± 0·04	0·51 ± 0·02	1·80 ± 0·04	0·48
Male	1·02 ± 0·04	0·52 ± 0·02	1·95 ± 0·03	0·45

Cytheretta buttensis reticulata subsp. nov.

(Pl. 15, figs 1–8; Text-fig. 21)

Derivation of name: Latin—reticulatus, net-like; refers to the ornamentation.

Diagnosis and description: Consists predominantly of Morphotype C together with Morphotypes A and B.

Holotype: Io 4032.

Paratypes: Io 4033–8.

Material: See Fig. 22.

Type locality and horizon: Cormeilles-en-Parisis; Bed no. 47 of Mlle. Albissin, Couches de Sannois supèrieur.

Stratigraphical range and distribution: Couches de Sannois supèrieur-Marnes à Huîtres infèrieurs.

Dimensions: (Carapace);

	L	H	L/H	W
Female	0·85 ± 0·025	0·48 ± 0·01	1·79 ± 0·03	0·42
Male	0·97 ± 0·02	0·50 ± 0·01	1·94 ± 0·03	0·43

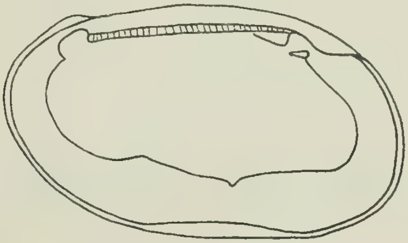

Fig. 21. *Cytheretta buttensis reticulata* sp. subsp. nov.; female left valve; ×75.

Discussion: Morphotype A resembles *C. bernesis* Oertli from the Rupelian of Switzerland; they differ in dorsal outline, as *C. bernesis* is tapered towards the anterior. The longitudinal ridges are also unequally developed in the latter; ridges no. 3 is strong, while nos. 4, 5 and 6 are weak, and they also form a slightly different pattern. *C. ramosa sublaevis* Triebel from the Chattian Cyrenenmergel of the Mainz Basin is similar, but the longitudinal ridges are very weak and can hardly be seen in the right valve; the surface of the valve is also more uneven, with marked longitudinal swellings in the position of ridges nos. 4 and 9; these swellings are much more apparent in *C. ramosa ramosa* (Lienenklaus).

	SAMPLE NUMBER	MORPHOTYPE %			Subspecies of C.buttensis
		A	B	C	
COUCHES DE SANNOIS	22 (48)	100	—	—	buttensis
	23 (79)	33	19	48	reticulata
MARNES A HUITRES	24 (72)	23	7	70	

Fig. 22. Distribution of morphotypes of *Cytheretta buttensis* sp. nov. from Cormeilles. Note that the stratigraphical sequence has youngest at the bottom.

DISCUSSION OF THE SUPERSPECIES *C. TENUIPUNCTATA*

The stratigraphically arranged series of specimens from the Paris Basin shows certain trends. The earliest species, C. *minipunctata* sp. nov. and C. *buttensis* sp. nov. *buttensis* subsp. nov., have very weakly developed ridges with several rows of puncta between them. In the later species the ridges become stronger and the puncta in between them become larger with fewer rows, as in C. *tenuipunctata absoluta* and C. *tenuipunctata lirata.* In the latter the ridges are very strong and the pitting is reduced to a single row of large pits.

It is considered that the relationships suggested in Fig. 23 represent a possible phylogeny.

The barrier may be ecological rather than geographical *sensu stricto.* C. *minipunctata*, or something like it, is a possible ancestor of C. *tenuistriata* with its two recorded geographical sub-species.

It is interesting to note that in Switzerland the finely punctate species with weak ridges, C. *variabilis* and C. *bernesis,* occur at a stratigraphically lower horizon than C. *tenuistriata tenuistriata,* as in the Paris Basin. In the Mainz Basin these postulated early forms are not present, possibly because the Sannoisian is poorly exposed, but more likely because they were not present in the area; they have not been found in samples collected nor recorded in the works of Triebel, Stchepinsky and Gramann. In the Chattian of the Mainz Basin there are, however, two finely punctate forms, C. *ramosa ramosa* (Lienenklaus) and C. *ramosa sublaevis* (Triebel). The valve of the former has an uneven surface, similar to C. *variabilis,* and both of these are only tentatively included in the superspecies. C. *ramosa sublaevis* has a much smoother valve with fine punctae between weak ridges.

C. *stigmosa* Triebel has a similar ridge pattern, but varies in shape and has much larger pitting. The two must be closely related, however.

The L/H ratio of all the female left valves from the Paris Basin were averaged, and gave an answer of 1·79 ± 0·04.

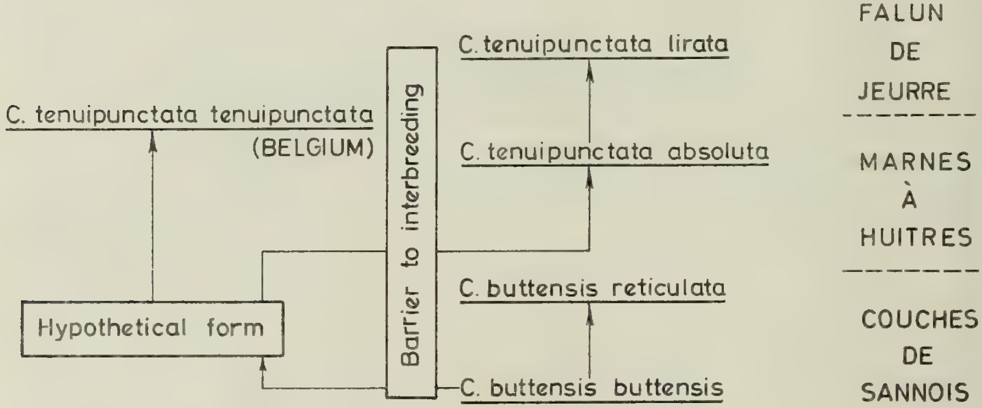
FALUN DE JEURRE
C. tenuipunctata lirata
C. tenuipunctata tenuipunctata
(BELGIUM)
Barrier to interbreeding
C. tenuipunctata absoluta
MARNES À HUITRES
C. buttensis reticulata
Hypothetical form
COUCHES DE SANNOIS
C. buttensis buttensis

FIG. 23. Suggested relationship between *Cytheretta buttensis* sp. nov. and *Cytheretta tenuipunctata* (Bosquet).

This standard deviation compares favourably with that of individual species, so it is concluded that this is a further character to be considered in diagnosing the superspecies.

C. minor (Lienenklaus), *C. stigmosa* Triebel and *C. regularis* sp. nov. show similarities to the superspecies *C. tenuipunctata* (Bosquet) in ornamentation, but differ in shape. *C. posticalis* Triebel has a similar shape to *C. tenuipunctata* but has almost no ornamentation.

Cytheretta minor (Lienenklaus)

(Pl. 16, fig. 6)

1905 *Cythereis jurinei* (von Munster) var. *minor* Lienenklaus, p. 32.
1952 *Cytheretta minor* (Lienenklaus) Triebel, p. 24, pl. 4, figs. 22–3.

DIAGNOSIS: A small species of the genus *Cytheretta* with smooth dorsal and antero-dorsal areas and double rows of puncta between weak ridges.

MATERIAL: 25 valves and carapaces from Weinheim (Trift). Io 3704.

TYPE LOCALITY AND HORIZON: Weinheim; Unterer Meeressand.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Mainz Basin, Unterer Meeressand; Paris Basin, Couches de Sannois supèrieur. Falun de Morigny.

DESCRIPTION: In the left valve there is a posterior hinge ear; the dorsal margin is very slightly convex and the greatest height is about one quarter of the way from the anterior. The anterior margin is obliquely rounded; the ventral margin is almost straight and the posterior margin is slightly tapered. In the right valve the dorsal margin is slightly convex and the ventral margin is concave. A few denticles are present along the anterior margin of the right valve. Ovate in dorsal view.

The dorsal and antero-dorsal regions are smooth, so that ridges no. 1 and 2 are absent. To the anterior of the sub-central plexus ridges b and c are prominent, but where ridge a would be is a diffuse area of puncta. There is a double row of puncta between the ridges. In most specimens the ridges are merely areas without puncta, but this gap between the double rows of pits is greater than that between the contained single rows. In a few specimens, however, actual ridges are present.

DIMENSIONS: (Carapaces).

	L	H	L/H	W
Female	0·88	0·53	1·66	0·45
Male	0·85	0·50	1·70	0·43

DISCUSSION: This could be included in the superspecies due to the similarity of the ridge pattern, even though ridge no. a is absent. The size seems to vary; the dimensions given by Triebel are less than those of the material examined from Weinheim, where it is the commonest *Cytheretta* species; those from the Paris Basin are in better agreement with Triebel. It shows a great resemblance to *C. tenuistriata tenuistriata* (Reuss), with which it is associated in the Mainz Basin. It is much smaller, however, and there are no specimens of intermediate size; it has a slightly different shape, and lacks ridge a.

Cytheretta posticalis Triebel

Diagnosis: A large species of *Cytheretta* with an elongate shape, sub-parallel dorsal and ventral margins, and prominent posterior hinge ear. It is almost smooth, with a faint ornamentation of ridges and puncta in the posterior and ventral parts of the valve.

Cytheretta posticalis posticalis Triebel

1905 *Cythereis jurinii* Lienenklaus (non von Münster), p. 31.
1952 *Cytheretta posticalis* Triebel, p. 23, pl. 3, figs 18–21.
1956 *Cytheretta posticalis* Triebel, Oertli, p. 59, pl. 6, figs 160–162.

Type locality and horizon: Welschberg (Mainz Basin), Unterer Meeressand.

Stratigraphical range and horizon: Mainz Basin: Unterer Meeressand, Schleichsand, Cyrenenmergel; Switzerland: Meeressand, Blaue Tone (both Rupelian).

Cytheretta posticalis parisiensis subsp. nov.

(Pl. 18, figs 1–4, 6)

Derivation of name: Named after Paris.

Diagnosis: A subspecies of *C. posticalis* showing a large amount of variation in areas of ornamentation.

Holotype: Io 4039.

Paratypes: Io 4040–42.

Material: 22 valves from Auvers-St.-George; 5 from Morigny.

Type locality and horizon: Auvers-St.-George, Stampian.

Stratigraphical range and distribution: Auvers-St.-George, Morigny; Stampian of the Paris Basin.

Description: Sexual dimorphism is pronounced, the males being more elongate. The left valve has a strong posterior hinge ear and a weak anterior one; this causes the dorsal margin to have an undulating appearance. This is particularly true of the male. The anterior margin is evenly rounded; the ventral margin, almost parallel to the dorsal, is slightly concave in the male and convex in the female. The posterior margin is tapered. In the right valve the dorsal margin is almost straight and the ventral is concave. It is ovate in dorsal view.

The ornamentation varies. Some specimens are completely smooth; some have a few faint double rows of puncta in the ventral portion of the postero-median region; others have a few faint ridges with puncta between in the postero-ventral angle.

The internal features are as for the superspecies *C. tenuipunctata* with inner margin similar to *C. tenuistriata ornata*.

Discussion: *C. posticalis posticalis* differs only in the ornamentation, which is restricted to a few ridges in the postero-ventral angle. Some specimens of

C. posticalis parisiensis are exactly the same, but the great variation within the sample is taken to indicate subspecific differentiation.

C. klahni Stchepinsky from the Stampian Marnes à Cyrènes of Alsace has ornamentation confined to the median and posterior parts of the valve and consists of double rows of small puncta. In this respect it is similar to some of the specimens of *C. posticalis parisiensis*. However, the lateral outline has a rhomboidal appearance due to the shape of the posterior margin, which differs from *C. posticalis*; and in dorsal outline it is more tapered. It is much smaller, but is probably a related species.

DIMENSIONS:

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·95	0·53	1·79	0·91	0·47	1·94
Male	1·05	0·53	1·98	1·03	0·49	2·10

Cytheretta headonensis Haskins

(Pl. 18, figs 11–14; Text-fig. 24)

1857 *Cytherideis colwellensis* Jones (pars) p. 49, pl. 14, figs 20a–c.
1870 *Cythere* ? Jones p. 157 and 159.
1887 *Xestoleberis aurantia* non Baird, var. Jones and Sherborn, vol. 4, p. 456.
1889 *Cytherideis colwellensis* Jones, Jones and Sherborn p. 45.
1968 *Cytheretta rhenana headonensis*, Haskins, p. 167, pl. 3, figs 11–18.

DIAGNOSIS: An unornamented species of *Cytheretta* with a strongly obliquely rounded anterior margin.

MATERIAL: 3 valves from Headon Hill; 16 from Colwell Bay; 17 from Milford; 7 from Whitecliff Bay. Io 4043–7.

TYPE LOCALITY AND HORIZON: Although there are grounds for believing that Headon Hill is the type locality due to etymology, in the type description Whitecliff Bay is quoted; Middle Headon Beds.

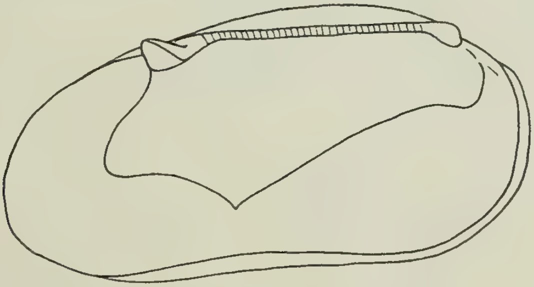

FIG. 24. *Cytheretta headonensis* Haskins; female right valve; ×75

Stratigraphical range and distribution: Middle Headon Beds of Headon Hill, Colwell Bay, Whitecliff Bay, and Milford.

Discussion: This is very similar to *C. rhenana* Triebel; the left valve of *C. headonensis* has a much more obliquely rounded anterior margin, as well as more anterior radial pore canals (34 compared with 27).

Jones figured two different ostracods as his new species *Cytherideis colwellensis*; all of the material is preserved in the British Museum (Nat. Hist.), No. I 6431 (13). Pl. 4, fig. 13 of Jones is a species of *Neocyprideis*, which has now been selected as the lectotype to avoid taxonomic complications, even though the type is a moult stage and thus not very satisfactory; fortunately it is a very common species so that its diagnosis is possible with topotype material of the adult.

Cytheretta vesca sp. nov.

(Pl. 17, figs 8, 9, 12)

Derivation of name: Latin—vescus, weak, little; refers to the fragile appearance of the carapace.

Diagnosis: A species of *Cytheretta* with a thin shell and a weak ornamentation consisting of rows of small puncta in the posterior and latero-ventral areas of the carapace.

Holotype: Io 4048, a female left valve.

Paratypes: Io 4049–51.

Material: 9 valves.

Type locality and horizon: Auvers-St.-George; Stampian.

Stratigraphical range and distribution: So far known only from the type locality.

Description: Sexual dimorphism is distinct, the males being more elongate; sex ratio 1 : 1. The left valve has a weak posterior hinge-ear and a convex dorsal margin; the anterior margin is obliquely rounded; the ventral margin is straight; the posterior margin is obliquely rounded, particularly in the female. The ventral margin of the right valve is concave. The carapace is ovate in dorsal view.

The ornamentation consists of a few indistinct rows of very small puncta in the posterior and latero-ventral areas of the carapace.

The hinge of the left valve has a small antero-dorsal lobe, although the corresponding antero-dorsal platform of the right valve is very prominent. The antero-ventral lobe is weak; the antero-median tooth is small. The postero-median swelling is prominent in lateral view, but cannot be seen in dorsal view. The anterior tooth of the right valve is large, projecting beyond the dorsal margin; the posterior tooth is equally prominent in dorsal view, but smaller in lateral view.

The selvage forms the anterior margin; along the ventral margin there is a prominent flange and a wide flange groove; there is a narrow flange groove along the posterior. A list is present. There are some 45 normal pore canals, but the number of radial pore canals could not be determined, nor could the shape of the inner margin.

DIMENSIONS:

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·73	0·42	1·74	0·72	0·37	1·95
Male	0·70	0·38	1·84	0·70	0·33	2·12

DISCUSSION: This differs from *C. rhenana* in having a weak ornamentation. The ornamentation is much weaker than that of *C. stigmosa*. It differs from both of these in shape; the dorsal margin of the left valve is more convex and the posterior margin is more obliquely rounded. The carapace ot *C. vesca* is much less massive than these.

Cytheretta stigmosa Triebel

DIAGNOSIS: A species of the genus *Cytheretta* with an obliquely rounded anterior margin. The ornamentation consists of longitudinal rows of large pits with ridges in between which become stronger ventrally.

Cytheretta stigmosa stigmosa Triebel

1952 *Cytheretta rhenana stigmosa* Triebel, p. 26, pl. 5, figs 28, 29.

TYPE LOCALITY AND HORIZON: Welschberg; Unterer Meeressand.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Rupelian Meeressand and Schleichsand of the Mainz Basin. Cavelier (1965, determinations by Apostolescu) records it from the Sannoisian of Sannois in the Paris Basin.

DISCUSSION: See *C. stigmosa gallica* sub sp. nov.

Cytheretta aff. ***stigmosa stigmosa***

(Pl. 16, fig. 8)

LOCALITY AND STRATIGRAPHICAL POSITION: Whitecliff Bay, Isle of Wight; Middle Headon, Beds (WB18). Io 4052.

DISCUSSION: Six poorly preserved specimens, together with one well preserved one, were available for study. No internal characters could be seen. The shape is similar to *C. stigmosa*. The ornamentation is very similar except that the pits are rather smaller and there are more of them per row than in *C. stigmosa stigmosa*. The dorsal and antero-dorsal regions are smooth. It is unknown whether this is a distinct subspecies or the same as that from the Rhine Valley.

Cytheretta stigmosa gallica subsp. nov.

(Pl. 17, Figs 1, 2, 5, 10; Text-fig. 25)

DERIVATION OF NAME: Latin—Gallica, country of the Gauls.

DIAGNOSIS: A subspecies of *C. stigmosa* in which the ornamentation covers the whole valve and the longitudinal ridges are very narrow.

HOLOTYPE: Io 4053, a female left valve.

PARATYPES: Io 4054–56.

MATERIAL: 44 valves, 4 carapaces.

TYPE LOCALITY AND HORIZON: Auvers-St-George; Stampian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: So far only known from the type locality.

DESCRIPTION: Sexual dimorphism can be observed, the males being more elongate; sex ratio, 1 : 1·5. The left valve has a posterior hinge ear; the dorsal margin is convex with the greatest height of the valve in line with the sub-central plexus. The anterior margin is obliquely rounded; the ventral margin is almost straight; the posterior margin is obliquely rounded, but only slightly so. In the right valve the ventral margin is concave.

Ridges with pitting between them are present in the ventral part of the valve and would correspond to ridges nos. 7–13 in the terminology adopted for *C. tenuipunctata*; ridges b and c can also be seen. In the median and dorsal areas are some seven longitudinal rows of large pits with weak and irregular ridges between them. There is an area of small pits, not arranged in rows, in the antero-dorsal region; to the anterior of the poorly defined sub-central plexus is an area of larger pits, while along the anterior margin there is reticulation.

In the hinge of the left valve the antero-dorsal lobe is slightly swollen; the antero-ventral lobe is small; the antero-median tooth is small but prominent; and the postero-median swelling is of equal size and prominence as the antero-median tooth.

The selvage runs close to the anterior and posterior margins so that there is only a very small flange groove present in these regions which is better seen in the right valve. Along the ventral margin of the right valve there is a wide flange groove.

The inner margin has a beak-shaped anterior indentation, prominent ventral, and a high and fairly narrow posterior indentation. The anterior segment is gently rounded, the median is short and curves into the steep posterior indentation. The distribution of pore canals could not be seen.

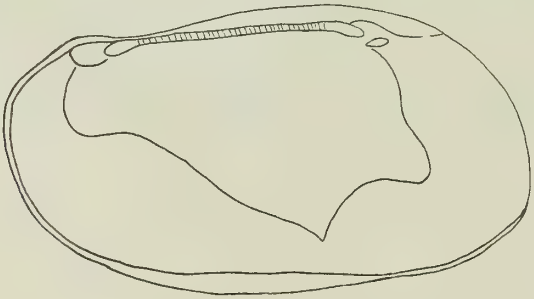

FIG. 25. *Cytheretta stigmosa* Triebel *gallica* subsp. nov.; male left valve; ×75.

DIMENSIONS:

	L	H	L/H	W
Female	0·75	0·47	1·57	0·38
Male	0·74	0·42	1·76	0·36

DISCUSSION: *C. stigmosa stigmosa* has unornamented dorsal and antero-dorsal areas and smaller pits with wider areas between the rows. Thus it differs from the almost reticulate appearance of *C. stigmosa gallica*. *C. minor* is rather similar but has double rows of puncta instead of single rows of large pits and unornamented areas as in *C. stigmosa stigmosa*; its lateral outline is also different. See also *C. regularis* sp. nov. and *C. bullans* sp. nov.

C. stigmosa is here regarded as a separate species rather than a subspecies of *C. rhenana* because the two are found together and should therefore be regarded as distinct species or as varieties or morphotypes of a single species. There is also a lack of intermediaries and the difference cannot be sexual because sexual dimorphism can be recognized with each group. It should be pointed out, however, that small unornamented forms and pitted forms similar to *C. rhenana* and *C. stigmosa* are found together not only in the Rhine Valley, but in the Paris Basin, Aquitaine Basin and the Hampshire Basin. They do not always occur in the same sample, but do occur at the same locality and in adjacent horizons. They perhaps inhabited different ecological zones and could represent ecologically separated subspecies. As this is not proven, the evidence still favours them as distinct species.

Cytheretta regularis sp. nov.

(Pl. 17, figs 3, 4, 6, 7; Text-fig. 26)

DERIVATION OF NAME: Latin—regularis, regular; refers to the smooth and regular lateral outline of the left valve.

DIAGNOSIS: A species of *Cytheretta* with a straight dorsal margin in the left valve, sub-parallel dorsal and ventral margins, and an evenly rounded posterior margin. Ornamentation consists of longitudinal rows of pits with a smooth antero-dorsal region. Sexual dimorphism is not pronounced.

HOLOTYPE: Io 4057.

PARATYPES: Io 4058–60.

MATERIAL: 12 valves and carapaces from Espibos, 6 from Lesbarritz.

TYPE LOCALITY AND HORIZON: Lesbarritz, Gaas (AGL1); Stampian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Lesbarritz and Espibos, Gaas; Stampian.

DESCRIPTION: Sexual dimorphism is not very pronounced, the males being slightly more elongate; sex ratio 1 : 2. The dorsal margin of the left valve is straight with no posterior hinge ear; the anterior margin is slightly obliquely rounded; the ventral margin is almost straight; and the posterior margin is evenly rounded. In the right valve the dorsal margin is convex and the ventral is concave. The dorsal and ventral margins are almost parallel. In dorsal view the carapace is ovate.

The ornamentation consists of 13 longitudinal rows of pits between narrow ridges. The sub-central plexus is fairly prominent although not appearing so in the electron scanning photographs, and to its anterior are two prominent ridges which slope towards the antero-ventral angle. The anterior and posterior regions are covered by numerous small pits. The extreme antero-dorsal area is smooth.

In the hinge of the left valve the antero-dorsal lobe is small and slightly swollen; the antero-ventral lobe is poorly developed; the antero-median tooth is small and the postero-median swelling is hardly noticeable. In the right valve the anterior tooth is much smaller and globose in shape.

The selvage is very close to the margins of the valve with a flange groove developed along the ventral margin and a small one along the posterior margin. The inner margin has three prominent indentations; the anterior one is rather ill defined in the specimens available, but is narrow; the ventral one is very long and narrow; the posterior one is small. The anterior segment is unevenly rounded; the median segment is short with a gentle curve; the posterior segment is long with a fairly steep slope. There are some 27 anterior radial pore canals, tending to be grouped into five sets; 35 closely spaced posterior radial pore canals; 10 ventral radial pore canals; and some 38 normal pore canals, which are not related to the ornamentation except that they mainly open into the pits of the outer surface.

The central muscle scars are in a slight pit with four equal small and circular adductor muscle scars along the posterior edge of the pit and a large frontal muscle scar on the anterior edge. The fulcral point is not very prominent.

DIMENSIONS:

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·70	0·38	1·84	0·68	0·35	1·94
Male	0·70	0·37	1·88	0·68	0·33	2·06

DISCUSSION: This differs from *C. stigmosa* in shape, particularly of the dorsal margin. The ornamentation is very similar to *C. stigmosa gallica* and also to *C. bullans*. It differs from the latter in the shape of the anterior margin, in size, and in the constancy of development of the ornamentation. It differs from *C. minor* in having single rows of large pits instead of double rows of puncta, as well as in shape.

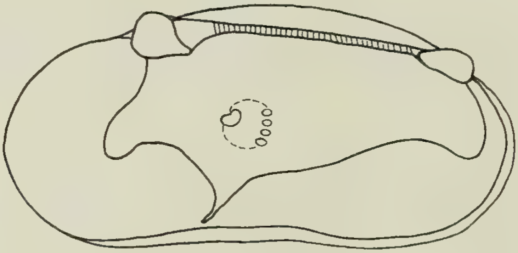

FIG. 26. *Cytheretta regularis* sp. nov.; male right valve; ×75.

Cytheretta bullans sp. nov.

(Pl. 18, figs 5, 7; Pl. 22, fig. 11)

Derivation of name: Latin—bulla, bubble; refers to the ornamentation which resembles strings of bubbles.

Diagnosis: A species of the genus *Cytheretta* with parallel dorsal and ventral margins and evenly rounded anterior and posterior margins. Ornamentation consists of longitudinal rows of pits often with a large unornamented anterior region.

Holotype: Io 4061.

Paratype: Io 4062.

Material: 18 carapaces.

Type locality and horizon: Chateau Romefort, Blaignan; Argile à Algues, Sannoisian.

Stratigraphical range and distribution: Known only from the type locality.

Description: Sexual dimorphism is distinct, the males being more elongate; sex ratio, 1 : 2. The dorsal and ventral margins of the left valve are parallel. The dorsal margin of the left valve is straight without a posterior hinge ear; the anterior margin is evenly rounded; the ventral margin is very slightly concave; the posterior margin is evenly rounded. In dorsal view it is ovate with a tapered anterior end.

The degree of development of the ornamentation varies. There are some thirteen rows of pits with ridges between to the posterior of the ill-defined sub-central plexus. To the anterior are two prominent ridges which slope towards the antero-ventral angle. There is an anterior area of reticulation with small pits in between. The antero-dorsal area is smooth. This unornamented anterior area varies in size; in some specimens the whole anterior area is smooth and in others the ornamentation is restricted to six or seven rows of pits in the postero-median position. It must be emphasized that this is not a form of sexual dimorphism, as might be inferred from Pl. 18, figs 5, 7.

Internal characters could not be seen.

Dimensions: Carapace

	L	H	L/H	W
Female	0·85	0·48	1·77	0·43
Male	0·90	0·45	2·00	0·40

Discussion: See *C. regularis*. It differs from *C. stigmosa* in lateral shape, and from *C. minor* in having single rows of large pits instead of double rows of puncta, as well as in shape.

Cytheretta sagri Deltel

Diagnosis: A species of *Cytheretta* with thirteen longitudinal ridges, often only present in the posterior. The inner margin has a characteristic shape with a depressed median segment markedly separated from the anterior and posterior segments.

Description: Six morphotypes divisible into three subspecies have been recognized; these are described below. The shape and ornamentation vary to a great extent, but the internal structures appear to be constant. Another feature that is constant is the five posterior spines.

The hinge of the left valve has a prominent swollen antero-dorsal lobe; a strong antero-ventral lobe; a large antero-median tooth; a very weak postero-median swelling, and a large posterior socket. In the right valve the anterior tooth is much larger than the posterior one.

The selvage runs very close to the anterior margin; a wide flange groove is present along the ventral margin with a narrow one along the posterior. The inner margin is very characteristic of the species. The anterior and posterior indentations are narrow; the ventral indentation is narrow and 'V'-shaped. The anterior and posterior indentations are semi-circular; the median segment is sharply differentiated from these, lying close to the ventral margin and with a postero-ventral indentation.

There are 25 anterior radial pore canals, 33 posterior, and 14 ventral. The central muscle scars are in a pit; the two lowest adductors are almost joined, and the frontal is inside the pit. The fulcral point is large and prominent.

Morphotype A:

Sexual dimorphism is pronounced, the males being more elongate. The left valve has a strong posterior hinge ear and a weak anterior one; the dorsal margin between these is symmetrically convex in the female and asymetrically convex in the male with the steep slope towards the posterior. The anterior margin is slightly obliquely rounded with some nine denticles in the ventral half. The ventral margin of the female is straight, while that of the male is concave. The posterior margin is evenly rounded. The dorsal margin of the right valve has a marked protuberance in the anterior half caused by the high position of the antero-median socket of the hinge; the ventral margin is concave. In dorsal view the female is ovate and tapered towards the anterior; the male is more bullet-shaped.

The ornamentation consists of thirteen longitudinal ridges. In the right valve ridges nos. 4 and 8 are sometimes very strong with a slight depression developed between them. Ridge no. 6 is thin, bifurcating at its anterior end just to the posterior of the sub-central plexus, one part joining no. 5 and the other no. 7. This ridge is always weak in the right valve, but in some left valves it is strong, stronger in fact than no. 7, so that it appears that no. 7 joins it instead of the other way round. To the anterior of the weak sub-central plexus are four prominent ridges sloping towards the antero-ventral angle. Faint cross-ridges and meandriform punctation are developed between the longitudinal ridges (see Pl. 21, fig. 5 for meandriform punctation).

Morphotype B:

This differs slightly from Morphotype A in shape; it has a more rectangular outline due to the evenly rounded anterior margin, and in dorsal view it is ovate, not tapered. The whole of the anterior margin is denticulate with some twelve denticles. The ornamentation is similar to that of Morphotype A, except that there is a smooth area of varying extent in the antero-dorsal region. The internal details could not be seen.

Morphotype C:

The female left valve has no anterior hinge ear, so the antero-dorsal angle is a smooth curve, unlike Morphotypes A and B. In dorsal view it is ovate. The ornamentation is restricted to the posterior part of the valve where 9–13 ridges can be seen. Ridge no. 6 is clearly recognizable and of equal strength to the other ridges. No internal details could be seen.

Morphotype D:

This is similar in shape to Morphotype C and the ornamentation is also restricted to the posterior. It differs in the inequality of the ridges; no. 6 in particular is weaker.

Morphotype E:

The female left valve has no anterior hinge ear, but the lateral outline of the carapace differs from Morphotypes C and D in being almost triangular with a very prominent posterior hinge ear. The carapace is unornamented over a large anterior and antero-dorsal area; longitudinal ridges are present over the remaining surface with a very fine meandriform punctation between them. Ridge no. 6 is very weakly developed. This differs from Morphotype B in shape and in having a much weaker ornamentation without the cross-ridges present between the longitudinal ridges.

Morphotype F:

This is very similar to Morphotype E, except that the ornamentation is restricted to the posterior half of the valve. Ridge no. 6 is very faint and thread-like, leaving a prominent gap between nos. 5 and 7; in this respect it differs from Morphotype C.

Cytheretta sagri sagri Deltel

(Pl. 19, figs. 1–4; text-fig. 28)

1964 *Cytheretta sagri* Deltel, p. 156, pl. 3, figs 56–57.

DIAGNOSIS AND DESCRIPTION: A subspecies of *C. sagri* consisting predominantly of Morphotype A with Morphotype D.

The last two larval stages have been recognized. The ornamentation in no. 8 consists of two prominent ridges, nos. 4 and 8 of the adult, with the other ridges of the adult stage weakly developed. Cross-ridges are sometimes present; puncta are present between the ridges. There are four posterior spines and eleven anterior denticles, each bearing one of the eleven anterior pore canals. In the seventh larval stage the two ridges nos. 4 and 8 are present. There are seven anterior radial pore canals and denticles and two posterior spines.

Material: See fig. 27. Io 4063–6.

Type locality and horizon: Lesbarritz, Gaas; Stampian.

Stratigraphical range and distribution: Stampian of Gaas (Lesbarritz Espibos) and Bastennes-Gaujacq, Aquitaine Basin.

Dimensions:

Morphotype A

	Left valve				Right valve		
	L	H	L/H	½W	L	H	L/H
Female	0·84	0·45	1·87	0·22	0·84	0·42	2·00
Male	0·90	0·47	1·91	0·24	0·90	0·43	2·09

Morphotype D (Carapace):

	L	H	L/H	W
Female	0·92	0·53	1·74	0·46

MORPHOTYPE SAMPLE	A	B	C	D	E	F	Subspecies of C. sagri
AGE 1	12						sagri
AGE 2	21						
AGL 1	1			4			
S 493	8	24	52				inconstans
RO 264				4	3		martini
RO 266						1	
RO 268					1	5	
RO 269					22	8	
RO 270						21	
RO 271				1	4	6	

Fig. 27. Distribution of Morphotypes of *Cytheretta sagri* Deltel.

Cytheretta sagri inconstans subsp. nov.

(Pl. 19, figs 5–7, 9)

Derivation of name: Latin—inconstans, the opposite of standing firm, or inconstant; refers to the great variation of shape and ornamentation.

Diagnosis and description: A subspecies of *C. sagri* showing variation in shape and ornamentation. The latter consists of thirteen longitudinal ridges which in some specimens cover the whole valve and in others only the posterior region. It consists predominantly of Morphotype C with A and B.

Holotype: Io 4067, a female left valve.

Paratypes: Io 4068–70.

Material: See fig. 27.

Type locality and horizon: Chateau Romefort, Blaignan; Argiles à Algues, Sannoisian.

Stratigraphical range and distribution: So far only known from the type locality.

Dimensions: Carapaces

	Morphotype B				Morphotype C			
	L	H	L/H	W	L	H	L/H	W
Female	0·78	0·43	1·81	0·38	0·92	0·53	1·74	0·47
Male	0·83	0·43	1·93	0·39	0·95	0·47	2·02	0·42

Cytheretta sagri martini subsp. nov.

(Pl. 20, figs 1–4)

Derivation of name: From the Phare St. Martin, Biarritz.

Diagnosis and description: A subspecies of *C. sagri* of a triangular shape in lateral view and with a weak ornamentation. It consists of Morphotypes D, E and F, particularly the last two.

Holotype: Io 4071, a female left valve.

Paratypes: Io 4072–6.

Material: See fig. 27.

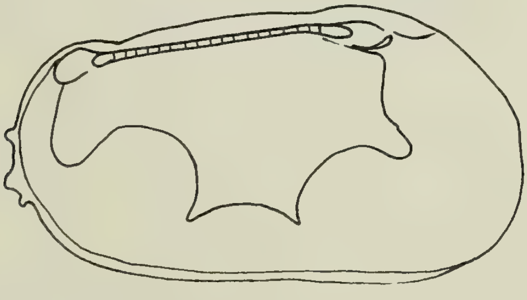

Fig. 28. *Cytheretta sagri* Deltel; female left valve. ×75

Type locality and horizon: Couches du Phare, Biarritz (RO 270); Stampian.

Stratigraphical range and distribution: So far only known from the type locality.

Dimensions:

Morphotype E

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·83	0·45	1·84	0·81	0·40	2·03
Male	0·86	0·45	1·91	0·90	0·43	2·09

Morphotype F (Carapace):

	L	H	L/H	W
Female	0·85	0·47	1·81	0·39
Male	0·87	0·45	1·93	0·40

Discussion: *C. sagri* Deltel may be the form described by Reuss (1869) as *Cythera multinervis* sp. nov. (p. 482, pl. 6, fig. 2).

The Oligocene of Aquitaine contains a group of closely related species: *C. sagri* Deltel, *C. gibberis* sp. nov., *C. minipustulosa* sp. nov., *C. postornata* sp. nov., and *C. samothracia* Deltel; *C. perita* Deltel from the Upper Eocene is perhaps related to this group.

C. sagri (Morphotype A), *C. minipustulosa* and *C. samothracia* have an unusual meandriform punctation between the longitudinal ridges, but the pattern of the ridges differs amongst the three species. *C. sagri* (Morphotypes C, D and G), *C. gibberis*, *C. perita* and *C. postornata* are similar in that the ornamentation is restricted to the posterior. *C. gibberis* differs in the unusual shape of the right valve with its dorsal "hump"; *C. perita* differs in shape in having only four posterior spines and in the shape of the inner margin; *C. postornata* also differs in shape and in ornamentation, which consists of six sulca, one of which reaches to the centre of the carapace.

C. tenuipuncta (Bosquet), *C. tenuistriata* (Reuss) and *C. buttensis* sp. nov. *reticulata* subsp. nov. are similar to *C. sagri* (Morphotype A), but have a different ridge pattern and lack the characteristic meandriform punctation. *C. buttensis reticulata* has cross-ridges similar to *C. sagri* (Morphotypes A and B), but differs by the features already mentioned. *C. posticalis* Triebel has the ornamentation restricted to the posterior, but this is much weaker than the ornamentation of *C. sagri* (Morphotypes C, D and G) and is developed in a more ventral position; it also differs in shape.

Cytheretta samothracia Deltel

(Pl. 21, figs 5, 6, 8)

1964 *Cytheretta samothracia* Deltel, p. 158, pl. 3, figs 58–60.

Diagnosis and description: Sexual dimorphism is pronounced; the female carapace is quadrate in lateral view, the male is rectangular. There are five prominent posterior spines. Ornamentation consists of eleven longitudinal ridges, including two prominent parallel ridges in the median part of the valve and two in the dorsal part. Between the ridges is a meandriform punctation and a faint reticulation.

MATERIAL: 36 valves and carapaces from Biarritz. Io 4077–79.

TYPE LOCALITY: Bastennes-Gaujacq; Stampian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Bastennes-Gaujacq, Lourquen; Stampian. Couches du Phare, Biarritz; Stampian.

DIMENSIONS:

	Left valve			Right valve		
	L	H	L/H	L	H	L/H
Female	0·95	0·56	1·70	0·95	0·49	1·94
Male	1·04	0·55	1·89	1·00	0·50	2·00

DISCUSSION: In shape and ornamentation this is easily distinguished from other species of *Cytheretta*. See also *C. sagri* and *C. minipustulosa*.

Cytheretta minipustulosa sp. nov.

(Pl. 21, figs 1–4; Text-fig. 29)

DERIVATION OF NAME: Latin—mini, small; pustulosa, full of pimples; refers to the ornamentation between the longitudinal ridges.

DIAGNOSIS: A species of *Cytheretta* with eleven longitudinal ridges, four of which join in the anterior to form two concentric ovals open towards the posterior. Between the ridges are faint cross-ridges and a meandriform punctation.

HOLOTYPE: Io 4080, a male right valve.

PARATYPES: Io 4081–83.

MATERIAL: 15 valves and carapaces from Biarritz; 1 valve from Gaas.

TYPE LOCALITY AND HORIZON: Biarritz; Couches du Phare superieur.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Couches du Phare, Biarritz (Stampian); Espibos (Gaas), Stampian.

DESCRIPTION: In lateral view the carapace is rectangular. Sexual dimorphism is not very pronounced, the males being more elongate. The left valve has a posterior

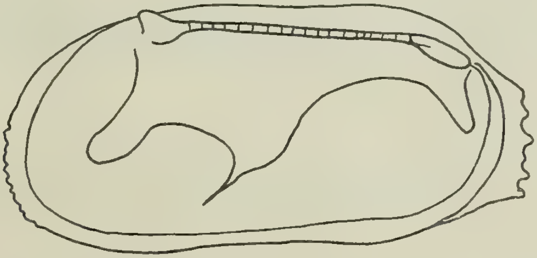

FIG. 29. *Cytheretta minipustulosa*; male right valve; ×75.

hinge ear and a weak anterior one; the dorsal margin between is slightly convex. The anterior margin is almost evenly rounded. The ventral margin is slightly concave, particularly in the male. The posterior margin is evenly rounded with five spines. In the right valve the dorsal margin has a protuberance due to the high position of the antero-median socket. The ventral margin is concave; the posterior has five spines, and there is a marked concavity in the postero-dorsal angle. In dorsal view the female is tapered, while the male has more or less parallel sides.

Ornamentation consists of eleven longitudinal ridges. Ridges nos. 2 and 6, and nos. 3 and 5 join in the anterior and form two concentric ovals, open towards the posterior. Ridge no. 4, which is weak, runs down the centre. Nos. 5 and 6 join towards the posterior. Between the longitudinal ridges are faint cross-ridges and a meandriform punctation. There is no sub-central plexus.

The hinge of the left valve has a swollen antero-dorsal lobe; a strong antero-ventral lobe; a deep anterior socket; a small antero-median tooth; and a weak postero-median swelling. In the right valve the anterior tooth is large and pointed; the posterior tooth is small.

The selvage is strong. It runs close to the anterior margin but a small flange groove is present; the flange groove along the ventral margin is not large. The selvage is very strong in the posterior forming a projecting ridge, to the posterior of which is the flange groove. The latter has more the appearance of a platform; the flange is weak.

The inner margin has a characteristic shape. The anterior and posterior segments are narrow and deep; the ventral indentation is small, but because of the shape of the posterior segment it is very prominent. The anterior segment is semi-circular; the median segment is small and overshadowed by the steeply curved posterior segment, which sweeps up close to the dorsal margin.

The two lower adductor muscle scars touch; the third is elongate; the topmost one is triangular. The fulcrum is not very prominent. No pore canals could be seen.

DIMENSIONS:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·88	0·48	1·83	—	0·98	0·48	2·04
Male	1·00	0·48	2·08	0·40	1·09	0·50	2·18

DISCUSSION: This differs from *C. sagri* Deltel by the ridges which form two concentric ovals open towards the posterior, in its elongate shape, and in the shape of the inner margin. It differs from *C. samothracia* Deltel in lacking the two sets of paired ridges, as well as in its more elongate shape.

Cytheretta gibberis sp. nov.

(Pl. 16, figs 9, 10; Pl. 19, figs 10)

DERIVATION OF NAME: Latin—gibberis, hump on the back; refers to the shape of the female right valve.

DIAGNOSIS: A species of *Cytheretta* in which the right valve of the female is very high in the posterior. Ornamentation is restricted to the posterior and consists of twelve radial sulca, the central one being longer than the others.

HOLOTYPE: Io 4084, a female right valve.

PARATYPES: Io 4085–86.

MATERIAL: 9 valves and carapaces.

TYPE LOCALITY AND HORIZON: Couches du Phare superieur (RO 271), Biarritz.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: So far only known from the type locality.

DESCRIPTION: Sexual dimorphism is distinct, particularly in the right valve. The left valve has a weak posterior hinge ear, in front of which is a slight concavity; the remainder of the dorsal margin is convex. The anterior margin is obliquely rounded; the ventral margin is straight; the posterior margin is evenly rounded with a few small spines. The right valve of the female has a very high posterior dorsal margin, which over-reaches the left valve in the position of the concavity adjacent to the hinge ear. The dorsal margin slopes steeply to the position of the anterior tooth, in front of which is a concavity with the antero-dorsal platform of the hinge. The anterior margin is evenly rounded; the ventral margin is straight. The ventral part of the posterior margin bears some four spines, although the exact number could not be determined; in the dorsal part there is a large concavity. The right valve of the male is not so high posteriorly and has a concave ventral margin. In dorsal view the carapace is ovate.

The ornamentation is restricted to the posterior and consists of some eleven short, radiating sulca with a long central one which reaches to the central region of the carapace. There is a slight postero-ventral depression in the right valve.

Owing to the poor preservation of the material, the internal features could not be completely observed. The hinge of the left valve has a strong antero-dorsal lobe and a prominent antero-median tooth. The right valve has a large antero-dorsal platform and a large anterior tooth; the posterior tooth is fairly small and lies along the postero-dorsal concavity, almost at right angles to the dorsal margin.

The selvage is prominent with a wide flange groove along the anterior, ventral and posterior of the right valve. A weak list is present in the anterior and postero-ventral regions. The inner margin could not be clearly seen; the anterior and posterior indentations are deep and narrow; and the anterior segment is short and semicircular.

DIMENSIONS:

	Carapace				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·86	0·52	1·65	0·43	0·88	0·48	1·83
Male	—	—	—	—	0·92	0·47	1·96

DISCUSSION: The shape of the female right valve distinguishes this form from all other *Cytheretta* spp. in which the ornamentation is restricted to the posterior.

Cytheretta postornata sp. nov.

(Pl. 20, figs 5–8; Pl. 22, fig. 12)

Derivation of name: Latin—post, posterior; ornata, ornament; refers to the ornamentation which is restricted to the posterior.

Diagnosis: A species of *Cytheretta* in which the ornamentation is restricted to the posterior. This consists of 6–8 prominent sulca, one of which reaches to the centre of the carapace.

Holotype: Io 4087, a female left valve.

Paratype Io 4088.

Material: 10 carapaces.

Type locality and horizon: Biarritz; Couches de l'Atalaye (RO 264).

Stratigraphical range and distribution: So far only known from the type locality.

Description: Sexual dimorphism is not very strong. The dorsal margin of the left valve is strongly convex, less so in the right valve. The anterior margin is evenly rounded; the ventral margin is straight in the left valve, slightly concave in the right. The posterior margin is obliquely rounded and has five spines.

Ornamentation is restricted to the posterior half of the carapace and consists of some 6–8 sulca. These are mainly short, except for the central one which reaches to the centre of the carapace. Within this long sulcus is a fine threadlike ridge. No internal details could be seen.

Dimensions: Carapaces

	L	H	L/H	W
Female	0·83	0·49	1·69	0·43
Male	0·84	0·47	1·79	0·42

Discussion: This is similar to *C. sagri* Deltel (Morphotypes C, D and F), but differs from these in L/H ratio as well as ornamentation. *C. posticalis* Triebel has a completely different shape; *C. perita* Deltel differs in shape, L/H ratio, ornamentation, and has only four posterior spines.

Cytheretta perita Deltel

(Pl. 19, fig. 8)

1964 Cytheretta perita Deltel, p. 155, pl. 3, figs 53–55.

Diagnosis and description: The female is triangular in lateral view. There are some eight anterior denticles and four posterior spines. Ornamentation is restricted to the posterior, where there are six short ridges.

Material: 10 valves and carapace from Lespontes. Io 4089.

Type locality: Coupe de Lespontes, Peyrehorade; Bartonian.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Coupe de Lespontes (Moulin de Basat; Ferme Le Vigneau).

DIMENSIONS: Carapace

	L	H	L/H	W
Female	0·81	0·43	1·88	0·35

DISCUSSION: This differs from *C. posticalis* Triebel in shape, size, inner margin, and in having stronger posterior ridges. See also *C. postornata* sp. nov.

Cytheretta sculpta Ducasse

(Pl. 20, figs 9, 10)

1964 *Cytheretta sculpta* Ducasse, p. 225, pl. 1, figs 2–4.

DIAGNOSIS: A species of *Cytheretta* with a prominent anterior hinge ear in the left valve. The ornamentation consists of eleven longitudinal ridges with faint cross-ridges between them.

MATERIAL: 9 carapaces. Io 4090–91, Argiles à Algues, Blaignan.

TYPE LOCALITY AND HORIZON: Villeneuve-de-Blaye, Eocène supèrieur.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Upper Eocene and Sannoisian of the Bordeaux region.

DESCRIPTION: Sexual dimorphism is distinct, the males being more elongate. The dorsal margin of the left valve is slightly convex with a prominent anterior hinge ear. The anterior margin is obliquely rounded; the ventral margin is slightly concave; the posterior margin is evenly rounded. The right valve has a more typical *Cytheretta* shape due to the lack of the anterior hinge ear. There are some twelve denticles along the whole of the anterior margin and four spines along the posterior margin; these are present in both valves. The carapace is tapered towards the anterior end in dorsal view.

The ornamentation consists of eleven longitudinal ridges; nos. 2, 4, 7 and 10 run the whole length of the carapace; no. 1 forms the dorsal margin and in the left valve curves sharply downwards by the hinge ear to join no. 2. No. 3 is faint; no. 5 joins no. 4 just before the anterior margin; no. 6 is faint; no. 9 joins no. 8 in the centre. Another ridge is present just below the hinge ear of the left valve. There is a strong anterior marginal rim. Between the ridges are faint cross-ridges. There is no subcentral plexus.

No internal features could be seen. The antero-dorsal lobe of the hinge is very strong.

DIMENSIONS: Carapaces

	L	R	L/H	W
Female	0·70	0·40	1·75	0·33
Male	0·73	0·38	1·92	0·33

DISCUSSION: The ornamentation is unlike that of any other described species of *Cytheretta*.

Cytheretta sp. A

(Pl. 6, fig. 11)

Material: 1 carapace. Io 4092.

Locality and horizon: Moiselles; Sables de Beauchamp.

Dimensions:

Left valve, male: L, 0·74; H, 0·39; L/H, 1·90.

Discussion: This is very similar to *C. ruelensis* sp. nov.; the ridge pattern is the same, but the ridges are all of about equal strength. This is probably an individual of a species ancestral to *C. ruelensis*.

Cytheretta sp. B

(Pl. 9, fig. 12)

Material: 2 broken right valves, 2 distorted carapaces. Io 4093.

Locality and horizon: Biarritz: Couches à *Pentacrinus* de la Côte des Basques (RO 254; RO 255); Couches des Bains (RO 258).

Description: This has a posterior hinge ear in the left valve and four posterior spines. The ornamentation consists of eleven longitudinal ridges, one of which forms the dorsal margin; ridge no. 6 is short, not reaching to the anterior half of the valve. There is a strong anterior marginal rim and a wide anterior area of reticulation. A weak reticulation is present between the longitudinal ridges.

Dimensions:

Right valve: L, 0·75; H, 0·39; L/H, 1·92.

Discussion: This is of interest as the only *Cytheretta* sp. found in the Couches à *Pentacrinus*. There are no other species with which it can be compared.

Cytheretta sp. C

(Pl. 3, fig. 10)

Material: 1 right valve, L, 0·70.

Locality and horizon: Sables d'Auvers, Auvers-sur-Oise.

Discussion: The ornamentation of this valve is very similar to that of *C. bambruggensis* Keij, but it differs from the latter in having its greatest height situated more to the posterior. The specimen was unfortunately destroyed while being photographed with the electron scanning microscope, but is left here for the record.

Genus ***FLEXUS*** Neviani 1928

1928 Flexus, Neviani, p. 26.
1958 Eucytheretta Puri, p. 188.

Type species: *Cythere plicata* von Munster.

DIAGNOSIS: Similar to *Cytheretta* but with the development of three prominent longitudinal ridges. Ornamentation between the ridges varies. The carapace tends to be more elongate than *Cytheretta*.

DISCUSSION: See Introduction.

Flexus plicatus (von Munster)

(Pl. 22, fig. 1)

1830 *Cythere plicata* von Munster, p. 63.
1838 *Cythere plicata* von Munster, Roemer, p. 518, pl. 6, fig. 26.
1850 *Cypridina plicata* (von Munster), Ruess, p. 83, pl. 10, fig. 21.
1896 *Cythere plicata* von Munster, Lienenklaus, p. 141.
1952 *Cytheretta plicata* (von Munster), Triebel, p. 28, pl. 5, figs 34–35.
1956 *Cytheretta plicata* (von Munster), Oertli, p. 65, pl. 8, fig. 194.
1958 *Eucytheretta plicata* (von Munster), Puri, p. 188, pl. 3, figs 1–6.

TYPE LOCALITY AND HORIZON: Astrup, near Osnabruck; Upper Oligocene.

MATERIAL: 2 carapaces from Astrup. Io 4094.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: *F. plicatus* has been recorded from a great variety of localities and horizons. Authenticated occurrences however seem to be restricted to the Upper Oligocene of Astrup and Doberg.

DISCUSSION: This occurs together with a form resembling *F. concinnus* (Triebel); samples from the Upper Oligocene of Bühl near Weimer (Kassel) contain only the latter. This is the form figured and described by Speyer (1863, pl. 4, fig. 2) and mentioned by Lienenklaus (1894, p. 198).

Flexus concinnus (Triebel)

(Pl. 22, figs 2, 3, 5)

1852 *Cythere plicata* Bosquet (pars) (non von Münster), p. 60, pl. 2, fig. 13.
1895 *Cythere plicata* Lienenklaus (non von Münster), p. 17.
1905 *Cythereis plicata* Lienenklaus (non von Münster), p. 37, 64.
1952 *Cytheretta concinna* Triebel, p. 27, pl. 5, figs 31–33.
1957 *Cytheretta concinna* Keij, p. 132, pl. 10, fig. 6.

MATERIAL: Alzey: 10 valves; Auvers-St-George: 3. Io 4095–97.

TYPE LOCALITY AND HORIZON: Welschberg; Unterer Meeressand.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Unterer Meeressand of the Mainz Basin; Stampian of Jeurre, Auvers-St.-George, and Morigny in the Paris Basin; Sables de Berg and Argiles à *N. comta*, Belgium (Sables de Wemmel and Argiles d'Asche, Belgium ?).

Flexus gutzwilleri (Oertli)

(Pl. 22, fig. 4)

1956 *Cytheretta gutzwilleri* Oertli, p. 64, pl. 8, figs 189–192.

MATERIAL: 31 valves and carapaces from the topmost Couches du Phare (RO 270, 271). Io 4098–99.

TYPE LOCALITY AND HORIZON: Therwil (near Basel); Cyrenenmergel (Lower Chattian).

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Lower Chattian of Therwil; Couches du Phare, Biarritz.

Flexus solentensis sp. nov.

DERIVATION OF NAME: After the Solent.

DIAGNOSIS: A small species of the genus *Flexus* with a thick anterior marginal rim and thick longitudinal ridges.

Two subspecies have been recognized.

Flexus solentensis solentensis subsp. nov.

(Pl. 23, figs 7–10; Text-fig. 30)

1957 *Cytheretta gracilicosta* Keij (non Reuss), p. 135, pl. 10, fig. 5.
1968 *Cytheretta gracilicosta* Haskins (non Reuss), p. 166, pl. 3, figs 1—10.

HOLOTYPE: Io 4100, a female left valve.

PARATYPES: Io 4101–2.

MATERIAL: Barton: EBA 1 (Bed F), 4 valves; EHC 2 (Bed D), 2 carapaces. Alum Bay: Middle Barton Beds, 5 valves and carapaces.

TYPE LOCALITY AND HORIZON: Barton; Middle Barton Beds, Bed F.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Middle Barton Beds of Barton and Alum Bay.

DIAGNOSIS AND DESCRIPTION: Sexual dimorphism is distinct; sex ratio, 1 : 3 The left valve has a strong posterior hinge ear and a very weak anterior one; the

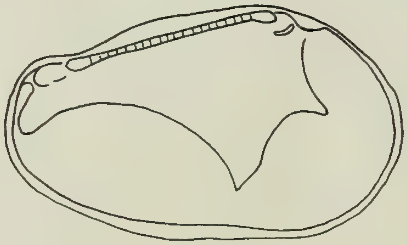

FIG. 30. *Flexus solentensis solentensis*; female left valve; ×75.

dorsal margin is convex. The anterior margin is almost evenly rounded; the ventral margin is concave, particularly in the right valve. The posterior margin is obliquely rounded. In dorsal view all three ridges can be seen, giving the carapace a tapered appearance with the apex at the anterior.

Ornamentation consists of three longitudinal ridges which end against a thick anterior marginal rim. The dorsal ridge forms the dorsal margin between the two hinge ears, curving downwards just to the posterior of the anterior hinge ear. The median ridge is roughly parallel to the dorsal ridge, but with a less accentuated course. The ventral ridge is almost straight. At the posterior the ventral ridge joins the median one and this remaining thin ridge then joins the thin posterior part of the dorsal ridge. Between the ridges is a coarse reticulation of irregular cross-ridges.

The hinge of the left valve has a small swollen, but very prominent, antero-dorsal lobe; the antero-ventral lobe is small; the antero-median tooth is large and the postero-median swelling is almost as big. In the right valve the anterior margin is pointed and the posterior tooth is almost equal in size. The inner margin does not appear to have a very well developed anterior indentation; the ventral and posterior indentations are narrow and deep. The median and posterior segments form a continuous steep curve, going a long way towards the dorsal margin.

There are 24 anterior, 22 posterior and 20 ventral radial pore canals. The selvage is prominent; there is a flange groove along the anterior, posterior and ventral margins; a list is developed in the antero-ventral and postero-ventral areas.

DIMENSIONS:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·52	0·31	1·68	0·25	0·51	0·27	1·89
Male	0·54	0·28	1·93	—	—	—	—

Flexus solentensis congestus subsp. nov.

(Pl. 23, figs 11–15)

DERIVATION OF NAME: Latin—congestus, dense, thick; refers to the longitudinal ridges.

HOLOTYPE: Io 4103, a female left valve.

PARATYPES: Io 4104–5.

MATERIAL: EBA 4, 7 valves and carapaces (5 females, 2 males).

TYPE LOCALITY AND HORIZON: Barton; Upper Barton Beds (Chama Bed, H).

STRATIGRAPHICAL RANGE AND DISTRIBUTION: So far only known from the type locality and horizon.

DIAGNOSIS AND DESCRIPTION: Shape and internal features are as for the nominate subspecies. The ornamentation consists of three very thick ridges which merge into a thick anterior marginal rim. The ridges are thicker than the intervening areas; the latter have a fine, uneven reticulation.

DIMENSIONS:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·51	0·30	1·70	0·24	0·51	0·25	2·04
Male	0·54	0·29	1·86	0·25	—	—	—

DISCUSSION: The oldest specimens of *F. solentensis* show similarities to *F. ludensis* sp. nov. in shape, size and ornamentation. In detail, however, the ridges are thicker and the reticulation between them consists of cross-ridges rather than the uneven reticulation of *F. ludensis*. They are quite probably related species however. In younger beds the ridges thicken until in the Upper Barton Beds the end member of the series is met with and is here distinguished as a separate subspecies, *F. solentensis congestus*. The remainder of the Barton Clay has not yielded any ostracods. The overlying Brockenhurst Beds contain a form of *F. ludensis* which must have migrated into the area with the Headon Beds transgression.

F. gracilicostus (Reuss) shows similarities to *F. solentensis* and *F. ludensis*, but has much finer ridges and a smaller and more even reticulation between them. In dorsal view it is more ovate and the three ridges do not stand out as in *F. solentensis* and *F. ludensis*. *F. gracilicostus* is also much larger.

Flexus ludensis sp. nov.

(Pl. 23, figs 1–6, 16)

DERIVATION OF NAME: After the Marnes à *P. ludensis* in which it is found.

DIAGNOSIS: A small species of the genus *Flexus* with thick longitudinal ridges; at the posterior the dorsal and ventral ridges join the median one; at the anterior the ridges join a strong marginal rim. Between the ridges is an uneven reticulation. At the posterior are three small spines.

HOLOTYPE: Io 4106, a female left valve.

PARATYPES: Io 4107–12.

MATERIAL: Verzy: PVY 2, 8 valves and carapaces; PVY 4, 22. Chavençon: PCC 2, 9 valves and carapaces. Whitecliff Bay: EWB(A), 2 valves and carapaces; EWB(B), 3; EWB 19, 2; EWB 22, 1. Headon Hill: EHH 42, 4 valves and carapaces.

TYPE LOCALITY AND HORIZON: Verzy; Marnes à *P. ludensis*.

STRATIGRAPHICAL RANGE AND DISTRIBUTION: Marnes à *P. ludensis* of Verzy and Chavençon. Brockenhurst Beds, Whitecliff Bay; Middle Headon Beds, Headon Hill, Whitecliff Bay.

DESCRIPTION: Sexual dimorphism is pronounced; sex ratio, 1 : 2·5. The left valve has a strong posterior hinge ear and a weak anterior one; the dorsal margin is convex. The anterior margin is almost evenly rounded with a few marginal denticles in the ventral portion. The ventral margin is straight in the anterior half, curving round into the posterior margin in the posterior half. The posterior margin is obliquely rounded and has three small spines in the median portion. The right valve has a concave ventral margin. In dorsal view all three ridges can be clearly seen, giving the carapace a tapered appearance with the apex at the anterior.

Ornamentation consists of three strong, prominent longitudinal ridges which end against a strong anterior marginal rim. The dorsal ridge forms the dorsal margin between the two hinge ears; it curves sharply downwards just to the posterior of the anterior hinge ear. The median ridge is slightly sinuous, running roughly parallel to the dorsal ridge but with a less accentuated course; it is very faint in the extreme posterior, but can be traced right to the margin, just before which it bifurcates. The ventral ridge is almost straight, curving upwards just before reaching the anterior marginal rim. All the ridges are faint at the posterior and tend to disappear amongst the reticulation, but the dorsal and ventral ridges appear to join the median ridge. The anterior marginal rim is particularly strong in the right valve. Between the ridges is an uneven reticulation; there is a particularly prominent "ridge" running between the median and dorsal ridges just to the posterior of centre. The specimens from the Headon Beds lack this "ridge". The area between the dorsal ridge and the antero-dorsal angle is almost smooth.

The hinge of the left valve has a swollen antero-dorsal lobe, prominent antero-ventral lobe, large antero-median tooth and a small postero-median swelling. In the right valve the posterior and anterior teeth are about equal in size and rather small. The selvage is prominent, with a small anterior and posterior flange groove and wide ventral one; the flange is particularly prominent along the anterior margin. A list is strongly developed in the antero-ventral and postero-ventral regions. No other internal details could be clearly seen.

DIMENSIONS:

	Left valve				Right valve		
	L	H	L/H	W	L	H	L/H
Female	0·50	0·30	1·67	0·23	0·51	0·26	1·96
Male	0·52	0·28	1·86	0·24	0·51	0·25	2·04

DISCUSSION: The specimens from the Headon Beds are slightly different from the Ludian ones, particularly with the reticulation between the ridges. The similarities are so strong, however, that it was thought unjustifiable to separate them. See also *F. solentensis* sp. nov.

Flexus lenijugum sp. nov.

(Pl. 21, figs 7, 9; Pl. 22, figs 9, 10)

DERIVATION OF NAME: Latin—lenis, smooth; jugum, ridge. Refers to the ornamentation.

DIAGNOSIS: A species of *Cytheretta* with an almost straight posterior margin bearing four spines; apart from the longitudinal ridges the carapace is smooth.

HOLOTYPE: Io 4113, a female left valve.

PARATYPE: Io 4114.

MATERIAL: 8 carapaces.

Type locality and horizon: Chateau Romefort, Blaignan; Argiles à algues.

Stratigraphical range and distribution: So far only known from the type locality.

Description: Sexual dimorphism can be discerned, but it is not very prominent. There are anterior and posterior hinge ears in the left valve; the dorsal margin is evenly rounded; the ventral margin is slightly concave in the left valve and strongly so in the right; the posterior margin is almost straight and has four spines. It is tapered towards the anterior in dorsal view.

The ornamentation consists principally of three longitudinal ridges. The dorsal ridge forms the dorsal margin; in the right valve it is continuous with the anterior margin rim; in the left, it ends beneath the anterior hinge ear. The median ridge is short and has another weak ridge above it in the posterior. The ventral ridge is strong, joining the anterior marginal rim and, at the posterior, the weak ridge above the median ridge. The anterior marginal rim is strong, running from the anterior hinge ear to the ventral margin.

No internal features could be seen.

Dimensions: Carapaces

	L	H	L/H	W
Female	0·80	0·43	1·86	0·38
Male	0·80	0·41	1·95	0·37

Discussion: *F. lenijugum* resembles *F. plicatus* (von Münster) with the lack of ornamentation between the longitudinal ridges. It differs in shape; *F. plicatus* has a more tapered posterior margin in lateral view. It also differs in the configuration of the ridges; the dorsal ridge does not form the dorsal margin in *F. plicatus*, nor does it join the anterior marginal rim; the ventral ridge is continuous with the anterior marginal rim, not merely joining it. *F. lenijugum* differs from all other described species by the absence of ornamentation between the ridges.

Flexus schoelleri (Keij)

(Pl. 22, figs 6–8)

1955 *Paracytheretta schoelleri* Keij, p. 119, pl. 16, fig. 4; pl. 19, figs 11–12.
1956 *Cytheretta schoelleri* (Keij) Oertli, p. 65, pl. 8, figs 196–197.
1965 *Protocytheretta schoelleri* (Keij) Moyes, p. 56, pl. 6, fig. 13.
1969 *Protocytheretta schoelleri* (Keij) Carbonnel, p. 111, pl. 8, figs 1–3.

Material: Couches du Phare: RO 269, 10 valves and carapaces; RO 270, 5; RO 271, 3. Io 4115–7. St. Geours-de-Maremne: ASG 1, 3 valves and carapaces; ASG 2, 2; ASG 3, 2.

Type locality and horizon: Moulin de Gamachot, Upper Aquitanian (?).

Stratigraphical range and distribution: Couches du Phare, Biarritz; Faluns Bleues, St. Geours-de-Maremne; Aquitanian and Burdigalian of the Bordelais and Rhone.

Discussion: This was placed by Puri (1958) into his new genus *Protocytheretta*, defined as 'Cytheretta'-shaped, but with three longitudinal ridges; *Flexus* was regarded as being 'Cythereis' shaped and with three longitudinal ridges. *F. schoelleri* has a truncated posterior margin which is not at all '*Cytheretta*'-like and the rod-like ridges are completely different from those of *P. daniana* (Brady). (See Hulings and Puri, 1964, p. 327 for an illustration of *P. daniana*.) *F. schoelleri* is probably not related to any other *Flexus* species here described, but is included in the genus on the purely morphological grounds that it has three longitudinal ridges.

The specimens from the Couches du Phare are smaller than the typical *F. schoelleri* (length of female carapace = 0·60 compared with 0·78).

Flexus sp. A

(Pl. 22, fig. 5)

Material: 1 carapace. Io 4118.

Locality and horizon: Bambrugge; Sables de Lede.

Dimensions: L, 0·64; H, 0·36; W, 0·31; L/H, 1·78.

Discussion: This is almost certainly a new species, but lack of material prevents a description. The configuration of the ridges is similar to *F. concinnus* (Triebel), but its shape is different from the latter both in dorsal and in lateral view, and it has a much stronger anterior marginal rim.

XV. CONCLUSIONS

The Cytherettinae have proven useful for helping to establish a correlation between the various localities in the Anglo-Paris-Belgian area in the Eocene and between this region and Germany in the Oligocene. In particular they support the idea of correlating the Sables de Lede with the Upper Lutetian of the Paris Basin, placing the Sables moyens in the Middle Eocene and correlating them with the Upper Bracklesham Beds of Hampshire, and correlating the Barton Beds with the Marnes à *P. ludensis*. Unfortunately the Cytherettinae provide little information concerning the relationship of the type Lattorfian with other areas of western Europe. The four species recorded from the Headon Beds suggest a relationship with the Bartonian on the one hand (*C. porosacosta*, *F. ludensis*) and with the Oligocene on the other (*C. headonensis*, *C.* aff. *stigmosa*), although the latter are related to the Eocene *C. carita* and *C. cellulosa*. Other ostracods however support a Bartonian age for the Headon Beds (Keen, 1968). Detailed correlation between England, France, and Belgium is possible using the evolution of *C. costellata* and *C. laticosta*.

The Aquitaine Basin formed a very distinct province, the only group in common with the northern areas being the *C. eocaenica* group. This suggests that the English Channel as now known could hardly have existed during the Eocene and Oligocene.

The presence of the Cytherettinae in Tertiary sediments is a good indication of shallow marine conditions, close to shore. Of the main species groups present, only the superspecies *C. laticosta* seems to have preferred muddy waters. The *C. haimeana* group were most abundant in clear waters in which calcareous or sandy sediments were accumulating, the *C. eocaenica*, *C. tenuipunctata*, *C. rhenana*, and *C. sagri* groups inhabited clear waters where sands were being deposited.

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PLATE 1

Cytheretta judaea (Brady)

FIGS 1, 4–7, 9. Specimens from Recent beach sand, Rimini.
FIG. 1. Left valve, female, Io 3807 × 70, L = 0·75 mm.
FIG. 4. Right valve, male, Io 3792, × 100, L = 0·79 mm.
FIG. 5. Right valve, male, Io 3810, × 70, L = 0·79 mm.
FIG. 6. Left valve, female, Io 3793, × 70, L = 0·75 mm.
FIG. 7. Enlargement of Io 3810 × 140.
FIG. 9. Posterior radial pore canals of Io 3793, × 100.

Cytheretta subradiosa (Roemer)

FIG. 8. Right valve, male. Io 3795 × 100, L = 0·81 mm, Lower Pliocene, Rimini.

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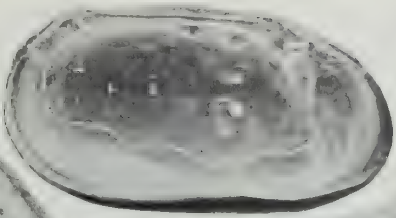
CORRIGENDA

Plate 2, caption to Fig. 8
For "punctuation" read "punctation".

Plate 15, caption to Fig. 10
For "Io 4031" read "Io 4030".

Plate 19, caption to Fig. 5-7, 9
For "Calcaire a Algues" read "Calcaire à Algues".



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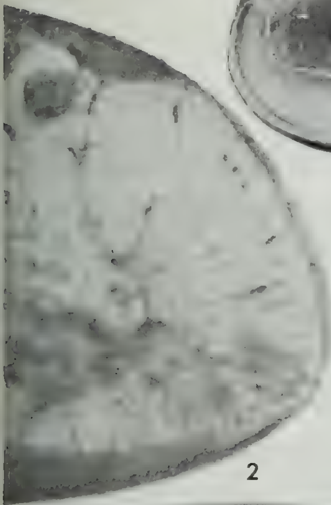

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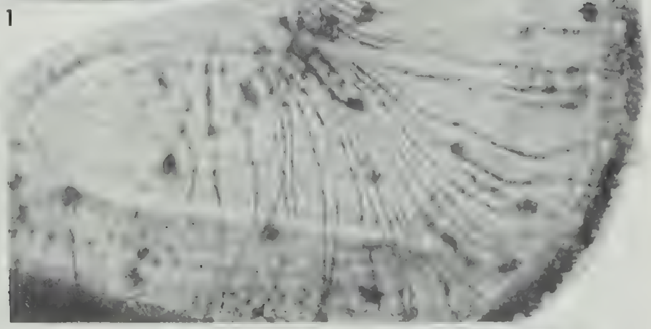

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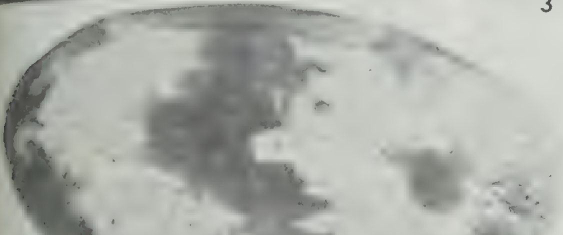

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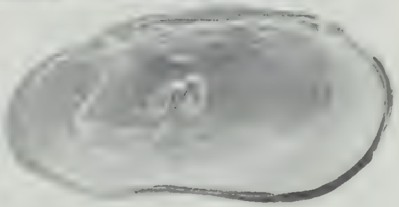

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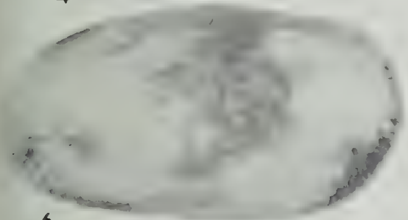

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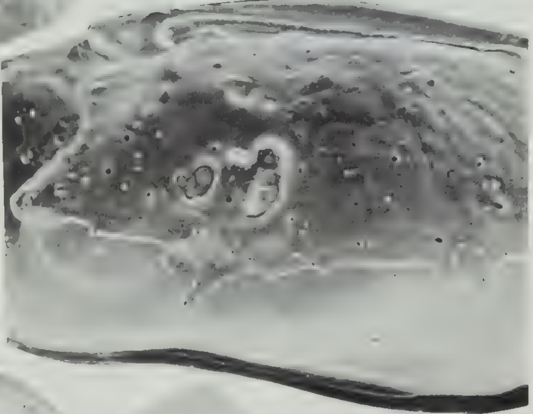

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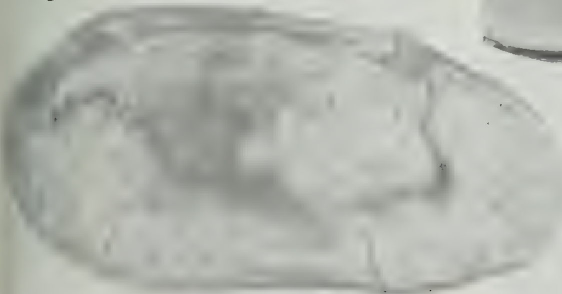

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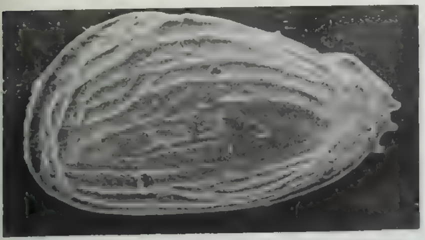
PLATE 2

All, except figs. 7, 8, × 70

Figs. 1–10 ***Cytheretta costellata costellata*** (Roemer)
Fig. 5 from Sables de Lede, Bambrugge; Fig. 6 from Upper Bracklesham Beds, Selsey; remainder from Lutetian IV, Damery. All except Fig. 5 are MORPHOTYPE A.

Fig. 1 Left valve, female, Io 3796, L = 0·69 mm.
Fig. 2 Left valve, male, Io 3798, L = 0·72 mm.
Fig. 3 Right valve, female, Io 3797, L = 0·69 mm.
Fig. 4 Right valve, male, Io 3799, L = 0·72 mm.
Fig. 5 Left valve, female, Io 3802, L = 0·72 mm. MORPHOTYPE B.
Fig. 6 Left valve, female, Io 3803, L = 0·64 mm.
Fig. 7 Detail of Io 3797, × 140
Fig. 8 Detail of Io 3797 showing " punctuation " between the ridges, × 300
Fig. 9 Female carapace, dorsal view, Io 3800, L = 0·70 mm.
Fig. 10 Male carapace, ventral view, Io 3801, L = 0·75 mm.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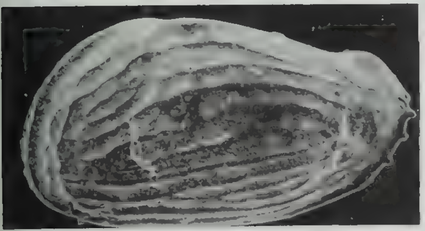
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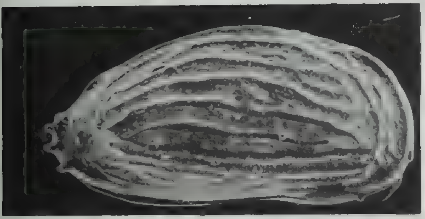
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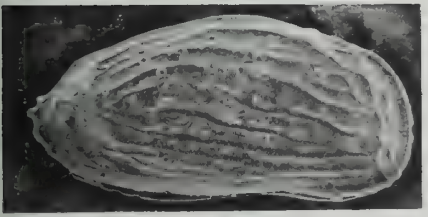
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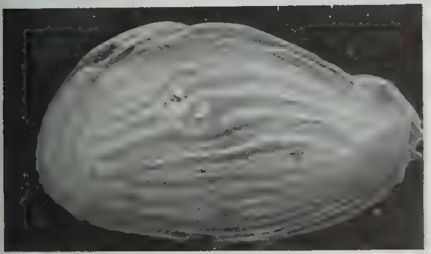
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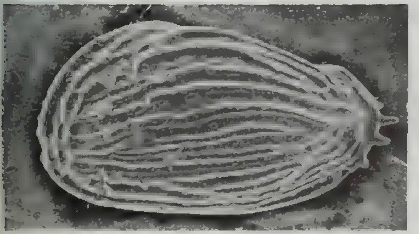
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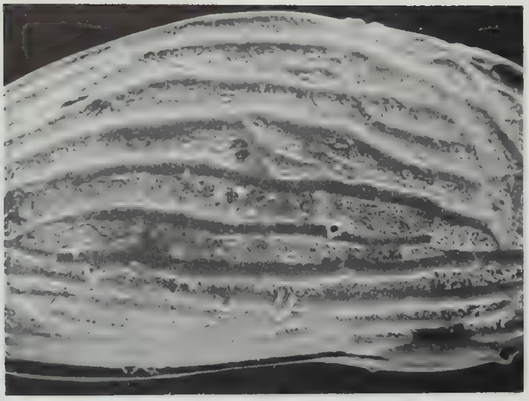
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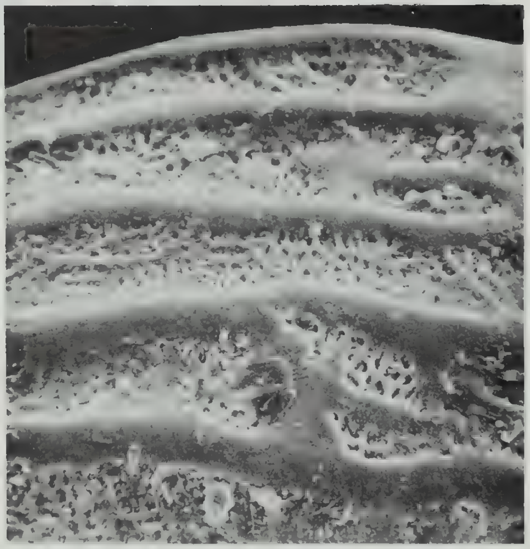
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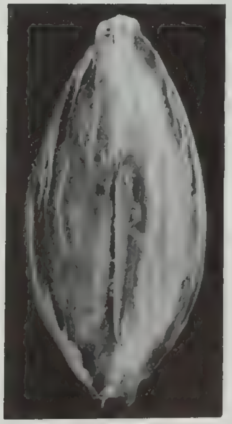
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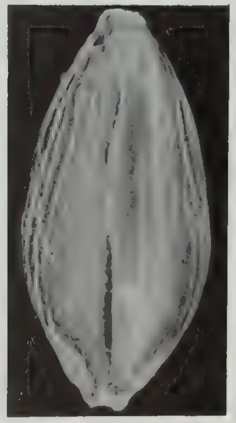
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PLATE 3

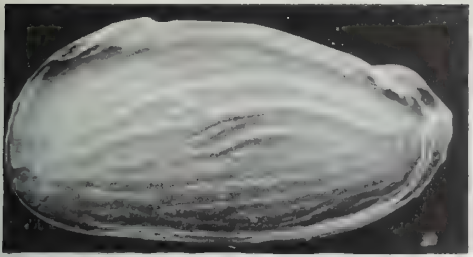
All, except Fig. 8, × 75

FIG. 1–8 ***Cytheretta costellata grandipora*** subsp. nov.

FIG. 1 MORPHOTYPE C, Left valve male, Io 3812, L = 0·83 Auvers-en-Oise.
FIG. 2 MORPHOTYPE, E. Right valve, female, Io 3811, L = 0·74 Auvers-en-Oise.
FIG. 3 MORPHOTYPE, D, Left valve, male, Io 3809, L = 0·83 Auvers-en-Oise.
FIG. 4 MORPHOTYPE, E, Right valve, female, Io 3805, L = 0·77 Moiselles.
FIG. 5 MORPHOTYPE, D, Left valve, female, Io 3808, L = 0·74 Auvers-en-Oise.
FIG. 6 MORPHOTYPE, E, Right valve, male, Io 3807, L = 0·85 Moiselles.
FIG. 7 MORPHOTYPE E, Left valve, female, Io 3804, L = 0·76 Moiselles.
HOLOTYPE
FIG. 8 Enlargement of Io 3804 showing " pores ". × 150.

FIG. 9 ***Cytheretta bambruggensis*** Keij. Right valve, female, Io 3827, L = 0·74. Sables de Lede, Bambrugge.

FIG. 10 ***Cytheretta*** sp. C. Right valve, female, L = 0·70 Auvers-en-Oise. Specimen destroyed.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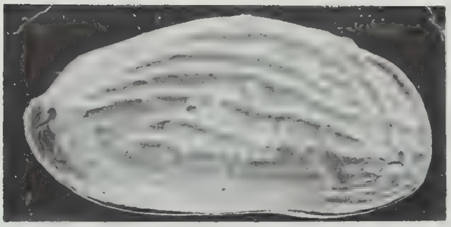
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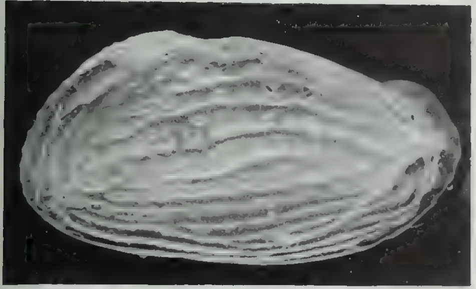
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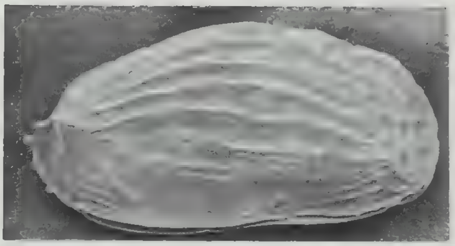
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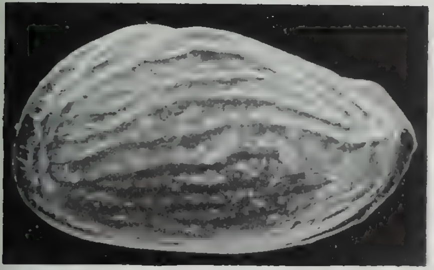
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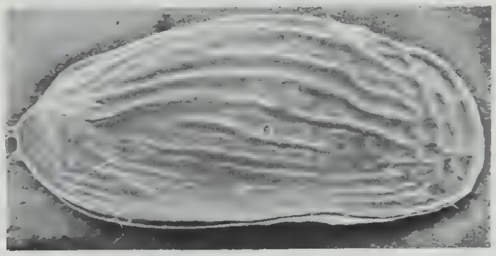
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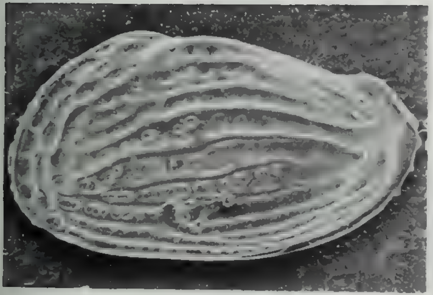
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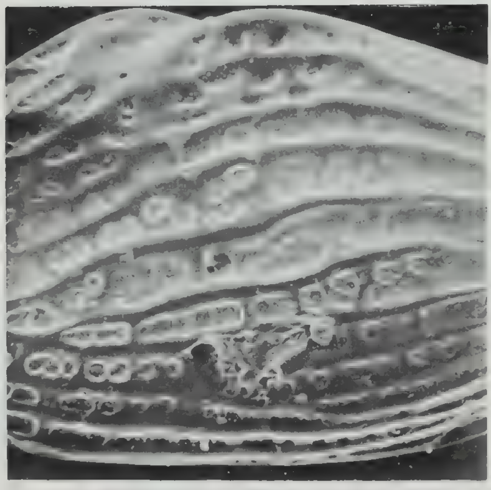
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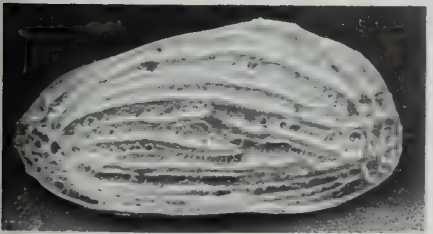
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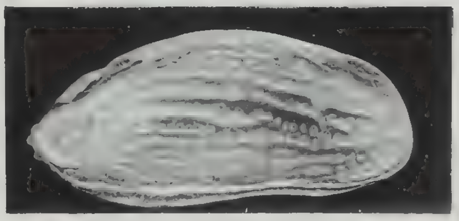
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PLATE 4

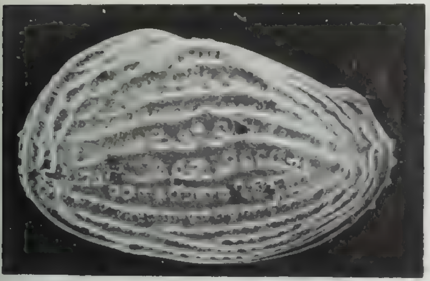
× 75

Fig. 1–8 ***Cytheretta costellata cratis*** subsp. nov. All specimens are MORPHOTYPE F from the Marnes à *P. ludensis*, Verzy.

Fig. 1 Left valve, female, Io 3814, L = 0·73 HOLOTYPE
Fig. 2 Left valve, male, Io 3817, L = 0·76
Fig. 3 Right valve, female, Io 3815, L = 0·70
Fig. 4 Right valve, male, Io 3818, L = 0·83
Fig. 5 Left valve, larval no. 8, Io 3820, L = 0·60
Fig. 6 Right valve, larval no. 8, Io 3819, L = 0·60
Fig. 7 Female carapace, ventral view, Io 3816, L = 0·73
Fig. 8 Male carapace, dorsal view, Io 3821, L = 0·76

Fig. 9–11 ***Cytheretta costellata antecalva*** subsp. nov. All specimens are MORPHOTYPE G from the Middle Barton Beds, Barton.

Fig. 9 Left valve, male, Io 3825, L = 0·84
Fig. 10 Left valve, female, Io 3823, L = 0·77. HOLOTYPE.
Fig. 11 Right valve, female, Io 3824, L = 0·77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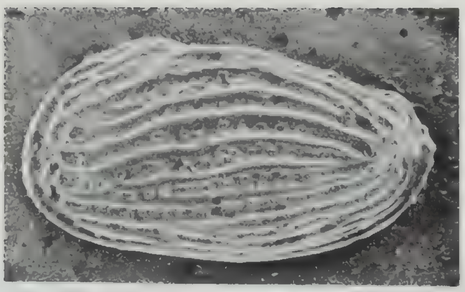
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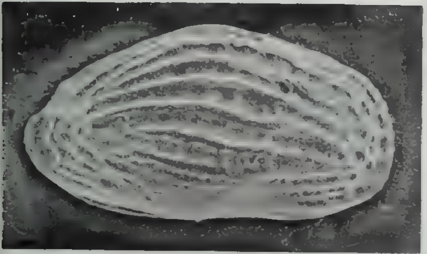
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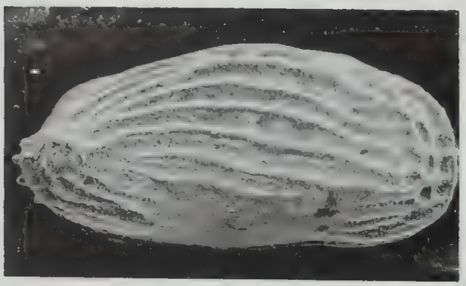
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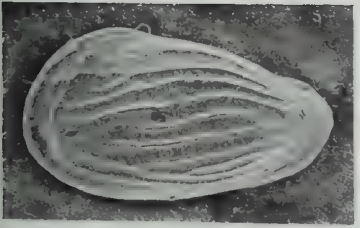
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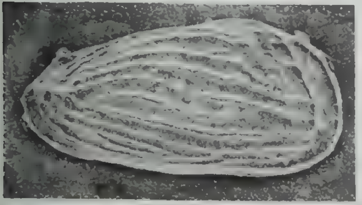
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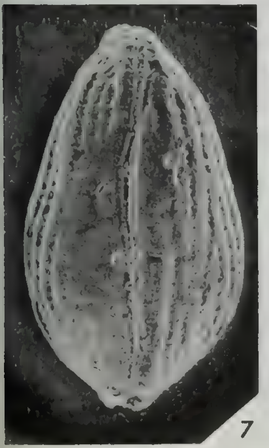
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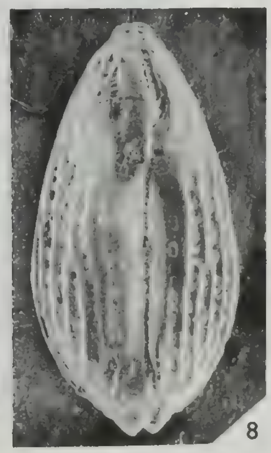
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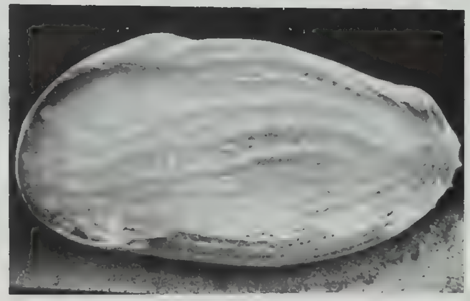
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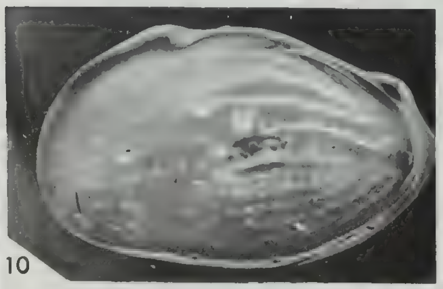
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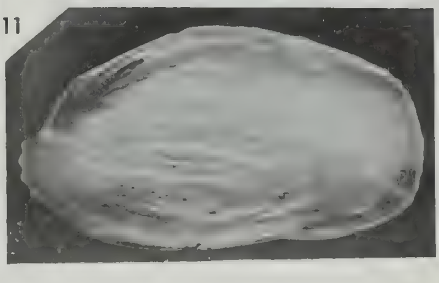
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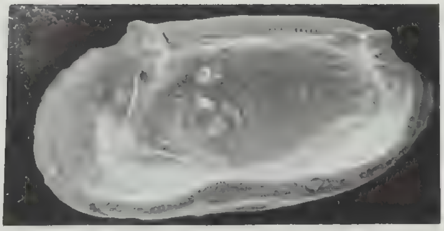
PLATE 5

FIG.	1–3	***Cytheretta costellata cratis*** subsp. nov.
FIG.	1	Right valve, female, Io 3822, L = 0·67, × 80, showing the inner margin. From the Marnes à *P. ludensis*, Chavençon.
FIG.	2	Hinge of Io 3822. × 400
FIG.	3	Central muscle scars and fulcral point of Io 3822. × 800.
FIG.	4–7	***Cytheretta ruelensis*** subsp. nov. Io 3837, Sables de Cresnes, Le Ruel. × 80. Female carapace. HOLOTYPE.
FIG.	4	Posterior view
FIG.	5	Dorsal view
FIG.	6	Left valve
FIG.	7	Right valve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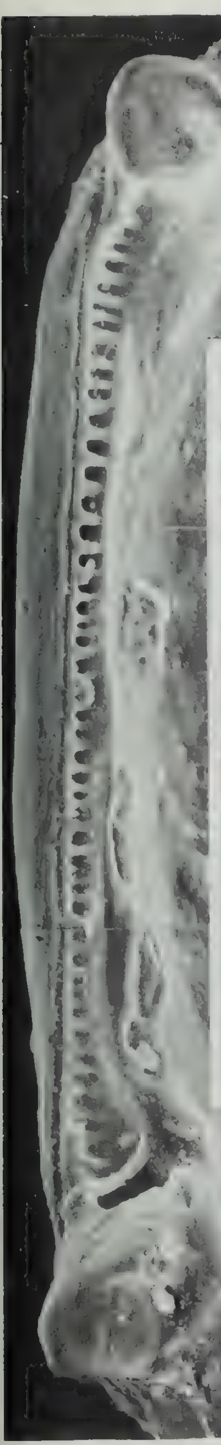
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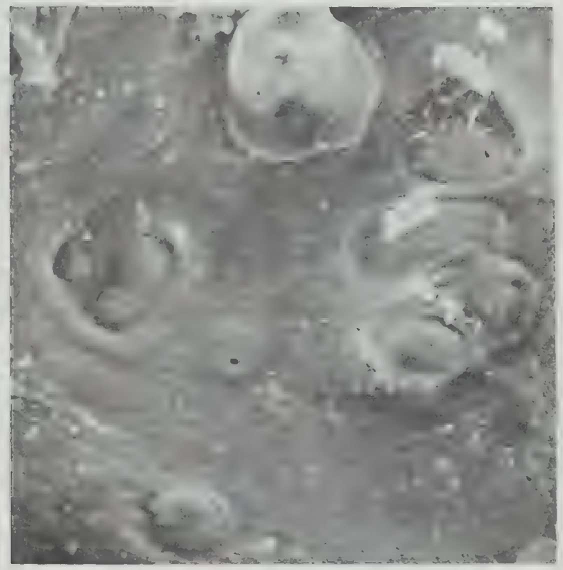
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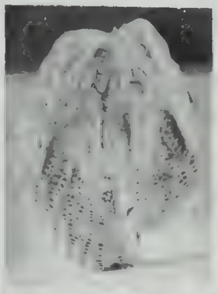
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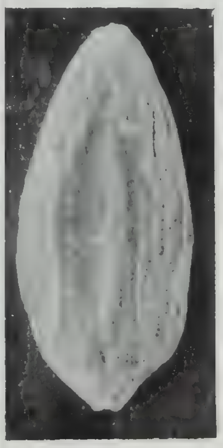
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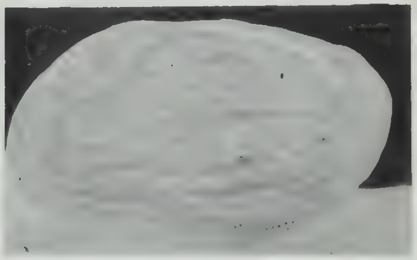
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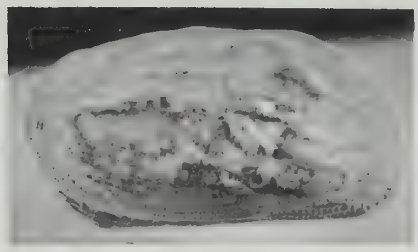
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PLATE 6

All × 70

FIG. 1, 6 ***Cytheretta haimeana*** (Bosquet)

FIG. 1 Left valve, female, Io 3834, L = 0·60. Lutetian IV, Damery.
FIG. 6 Left valve, female, Io 3835, L = 0·70. Sables de Beauchamp, Moiselles.

FIG. 2, 5 ***Cytheretta crassivenia*** Apostolescu.

FIG. 2 Left valve, female, Io 3828, L = 0·66. Lutetian IV, Damery.
FIG. 5 Left valve, female, Io 3829, L = 0·70. Sables de Beauchamp, Moiselles.

FIG. 3 ***Cytheretta*** aff. ***decipiens*** Keij
Left valve, female, of a carapace Io 3833, L = 0·66. Marnes à *P. ludensis*, Chavençon.

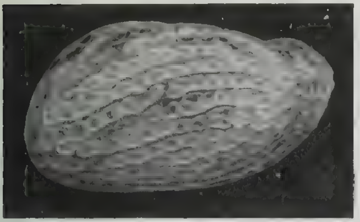
FIG. 4, 7 ***Cytheretta ruelensis*** sp. nov.

FIG. 4 Ventral view of male carapace, Io 3838, L = 0·85. Sables de Cresnes, Le Ruel.
FIG. 7 Left valve of Io 3838.

FIG. 8–10 ***Cytheretta decipiens*** Keij
Specimens from Sables de Beauchamp. Moiselles.

FIG. 8 Left valve, female, Io 3830, L = 0·69
FIG. 9 Left valve, male, Io 3832, L = 0·81
FIG. 10 Right valve, female, Io 3831, L = 0·73

FIG. 11 ***Cytheretta*** sp. A
Left valve, Io 4092, L = 0·74. Sables de Beauchamp, Moiselles.



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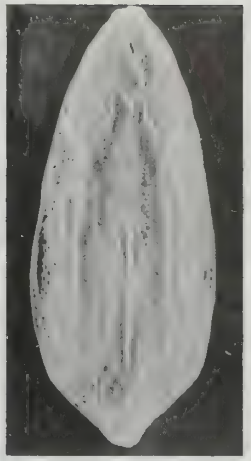

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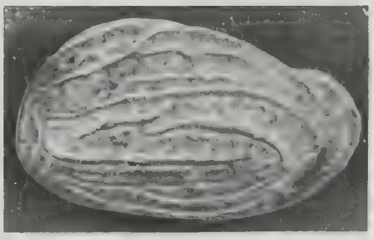

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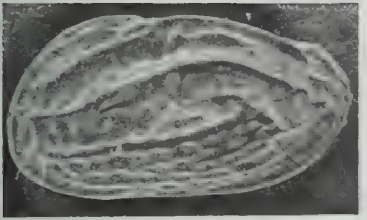

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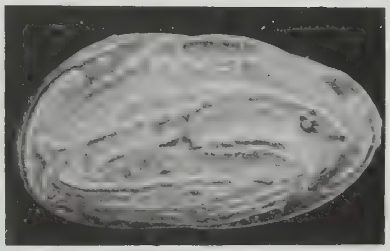

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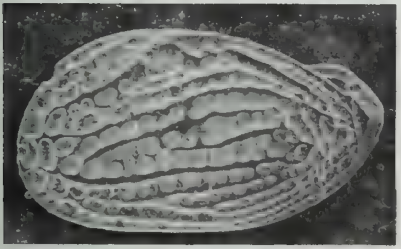

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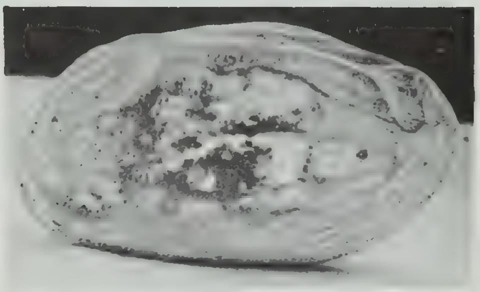

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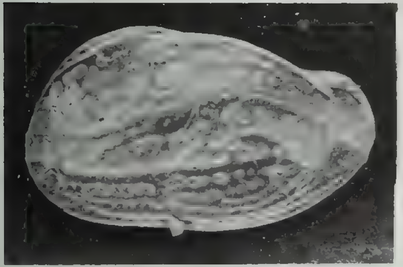

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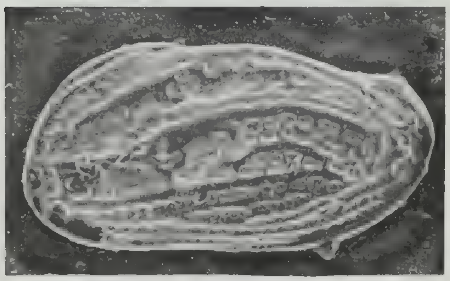

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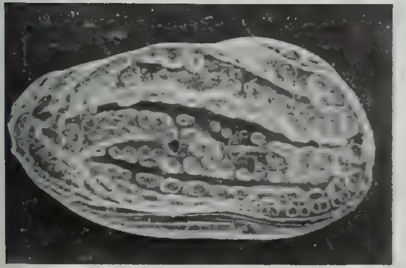

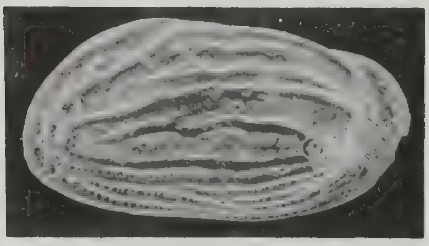

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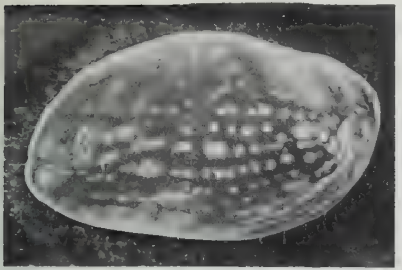
PLATE 7

Cytheretta eocaenica Keij

FIG. 6 from Lutetian IV, Damery; remainder from Sables de Lede, Bambrugge.

FIG. 1 Left valve, female, Io 3841, × 65, L = 0·79
FIG. 2 Left valve, male, Io 3844, × 65, L = 0·88
FIG. 3 Left valve, female, Io 3840, × 65, L = 0·88
FIG. 4 Hinge of Io 3844, × 125
FIG. 5 Central muscle scars of Io 3844, × 250
FIG. 6 Left valve, female, Io 3839, × 65, L = 0·80
FIG. 7 Right valve, male, Io 3842, × 65, L = 0·83
FIG. 8 Anterior tooth and hinge bar of Io 3844, × 650
FIG. 9 Left valve, female, Io 3843, L = 0·93. Post-maturation moult stage.
FIG. 10 Detail of pitting of Io 3839, × 750.



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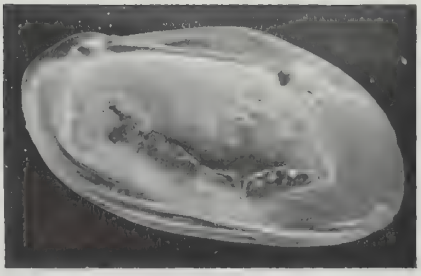

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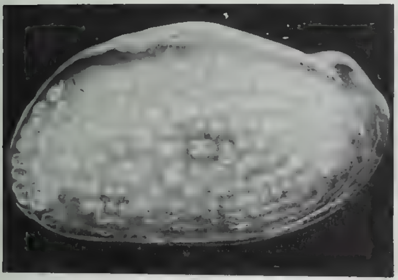

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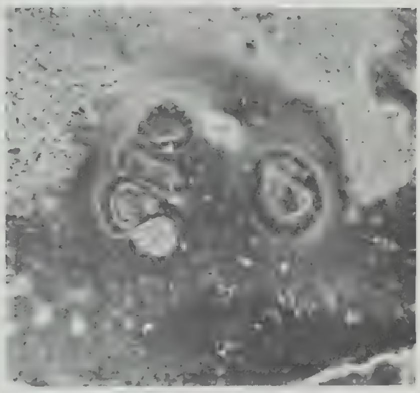

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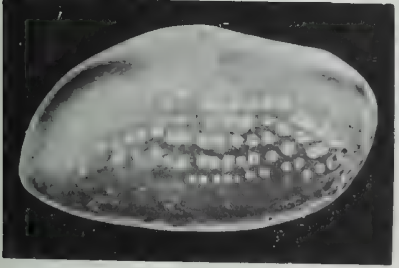

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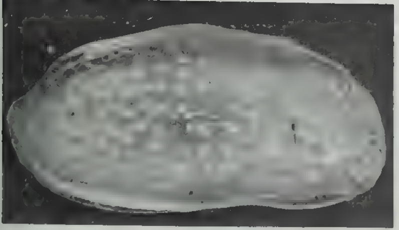

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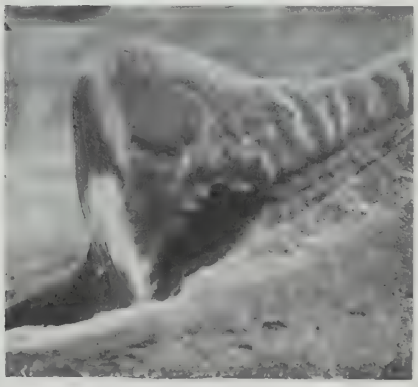

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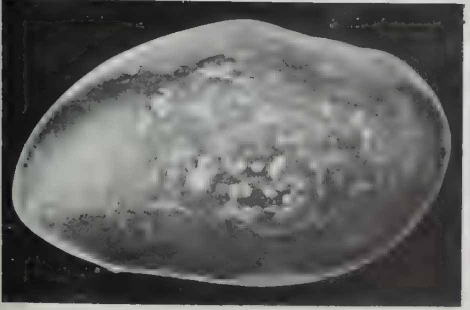

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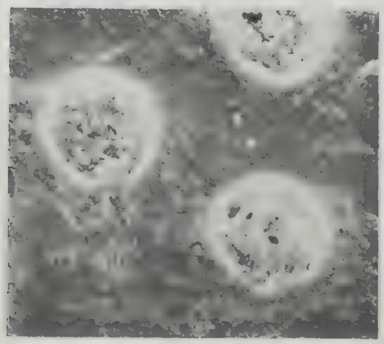

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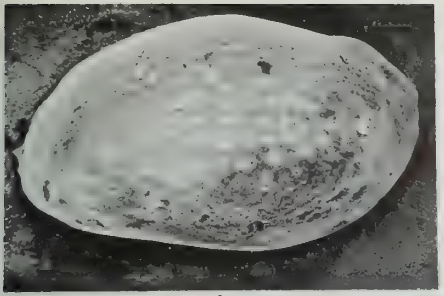
PLATE 8

Cytheretta oligocaenica sp. nov.

Specimens of Fig. 1, 2, 4 from the Couches du Phare, Biarritz; specimen of remaining Fig. from Faluns Bleues. St. Geours-de-Maremne.

Fig. 1	Left valve, female, Io 3845, × 70, L = 0·85, HOLOTYPE
Fig. 2	Carapace, dorsal view, male, Io 3847, × 70, L = 0·86
Fig. 3	Central muscle scars of Io 3849
Fig. 4	Right valve, female, Io 3846, × 70, L = 0·84
Fig. 5	Right valve, female, Io 3849, × 100, L = 0·84
Fig. 5	Right valve, female, Io 3849, × 100, L = 0·84
Fig. 6	Hinge of Io 3849, × 125
Fig. 7	Io 3849, × 70
Fig. 8	Anterior tooth of Io 3849, from dorsal, × 350
Fig. 9	Anterior tooth of Io 3849, from anterior, × 350
Fig. 10	Anterior tooth of Io 3849, from lateral view, × 350
Fig. 11	Posterior tooth of Io 3849, from ventral, × 350
Fig. 12	Posterior tooth of Io 3849, from posterior, × 350
Fig. 13	Posterior tooth of Io 3849, from lateral view, × 350.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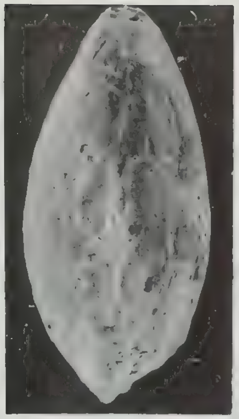
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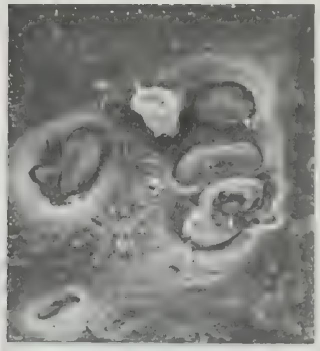
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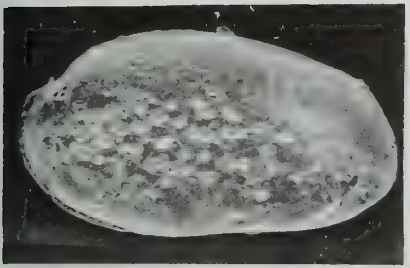
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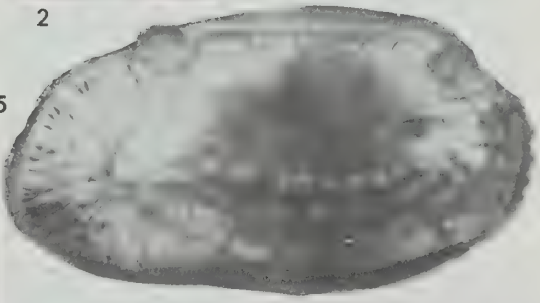
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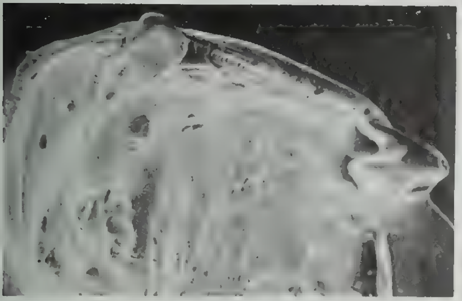
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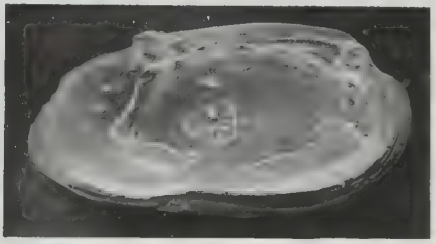
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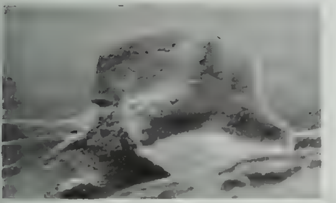
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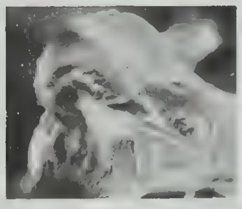
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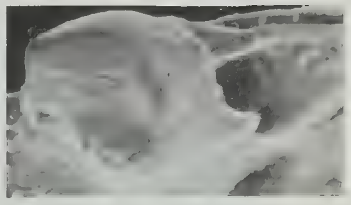
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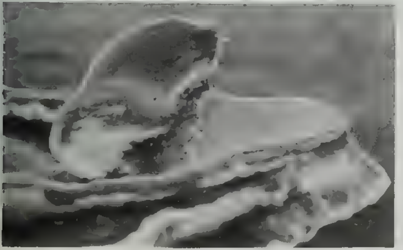
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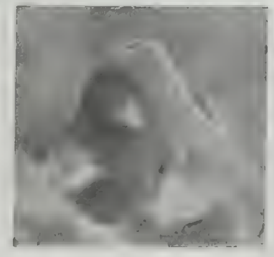
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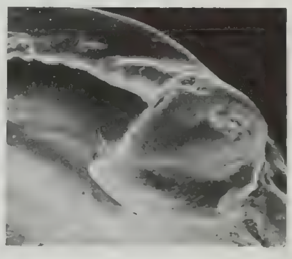
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PLATE 9

All × 70

FIG. 1–4, 6, 7 ***Cytheretta cellulosa*** sp. nov.

FIG. 2 from Sables de Beauchamp, Moiselles; remainder from Sables d'Auvers-en-Oise.

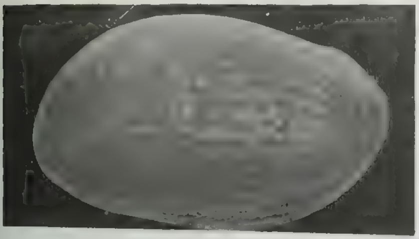
FIG. 1 Left valve, female, Io 3859, L = 0·78; HOLOTYPE
FIG. 2 Right valve, female, Io 3860, L = 0·74
FIG. 3 Left valve, male, Io 3861, L = 0·96
FIG. 4 Male carapace, dorsal view, Io 3863, L = 0·93
FIG. 6 Right valve, male, Io 3862, L = 0·93
FIG. 7 Posterior view of Io 3863.

FIG. 5, 8, 9–11 ***Cytheretta carita*** sp. nov.

Specimens from the Sables de Beauchamp, Moiselles.

FIG. 5 Female carapace, dorsal view, L = 0·87; specimen destroyed
FIG. 8 Female carapace, anterior view; specimen destroyed
FIG. 9 Left valve, female, Io 3853, L = 0·89; HOLOTYPE
FIG. 10 Right valve, female, Io 3854, L = 0·85
FIG. 11 Left valve, male, Io 3855, L = 0·94

FIG. 12 ***Cytheretta*** sp. B
Right valve, Io 4093; Marnes à *Pentacrinus*, Biarritz.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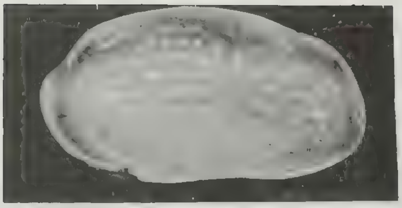
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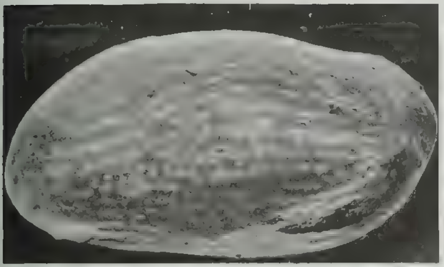
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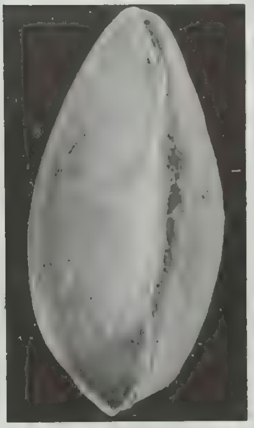
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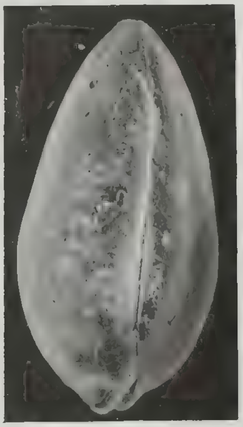
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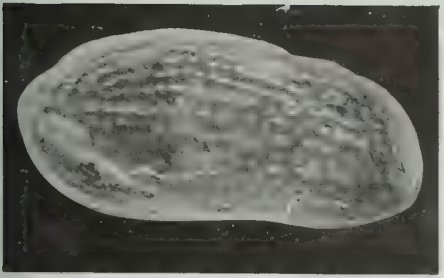
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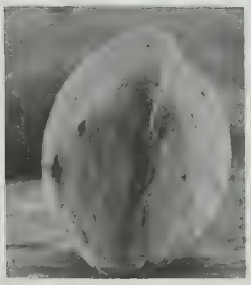
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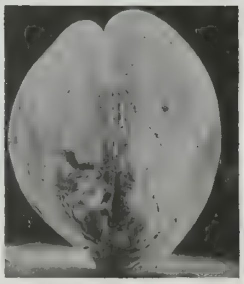
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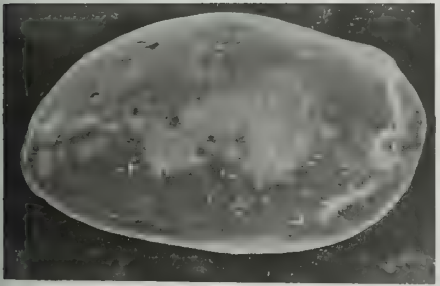
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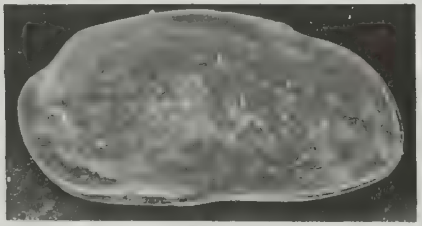
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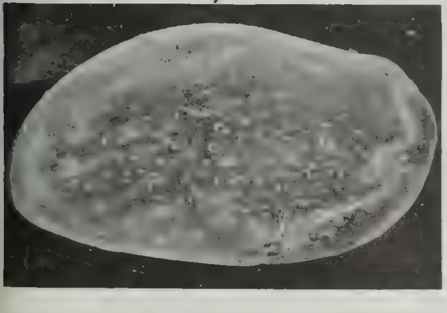
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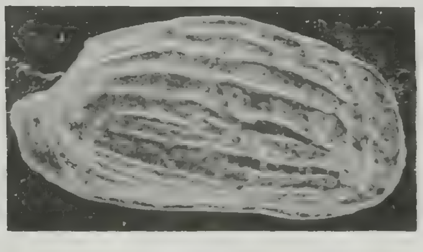
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PLATE 10

× 75

Cytheretta geoursenis sp. nov.

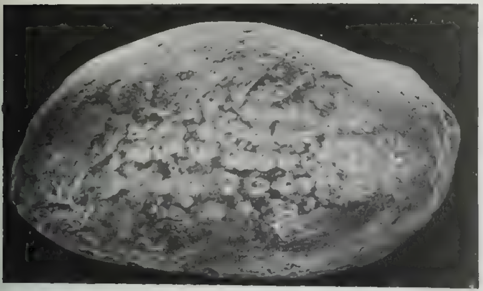
Specimens from the Faluns bleues, St. Geours-de-Maremne.

Fig. 1 Left valve, male, Io 3852, × 70, L = 1·07
Fig. 3 Left valve, female, Io 3850, × 60, L = 0·98; HOLOTYPE
Fig. 5 Right valve, female, Io 3851, × 70, L = 0·93

Fig. 2, 4, 6, 8, 9, ***Cytheretta laticosta*** (Reuss)
Specimens from the Middle Barton Beds, Barton.

Fig. 2 Left valve, female, Io 3865, × 70, L = 0·77
Fig. 4 Left valve, male, Io 3864, × 70, L = 0·90
Fig. 6 Right valve, male, Io 3866, × 70, L = 0·90
Fig. 8 Enlargement of Io 3864, central area between ventral and medium ridges, showing punctation. × 250.
Fig. 9 Further enlargement of Io 3864, showing a normal pore canal and surrounding puncta. × 850.

Fig. 7 ***Cytheretta carita*** sp. nov.
Male carapace, ventral view, Io 3858, × 70, L = 0·93; Sables de Beauchamp, Moiselles.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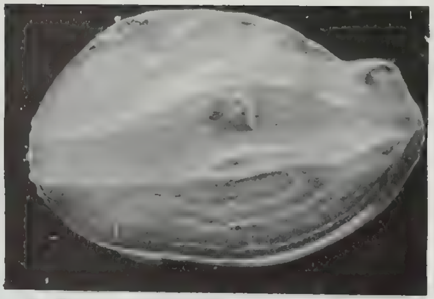
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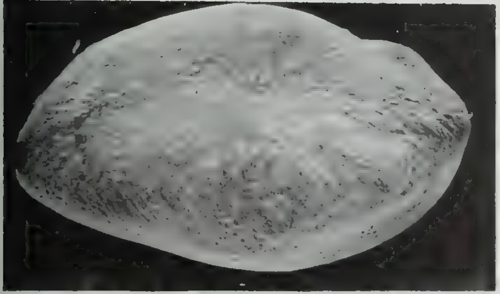
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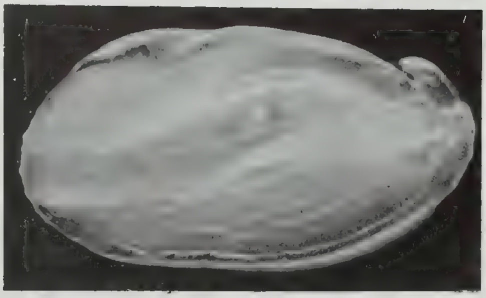
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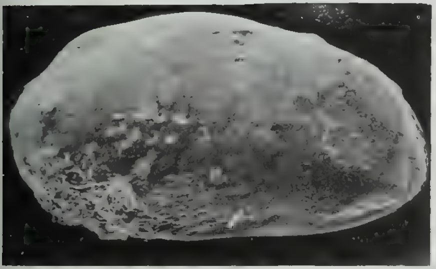
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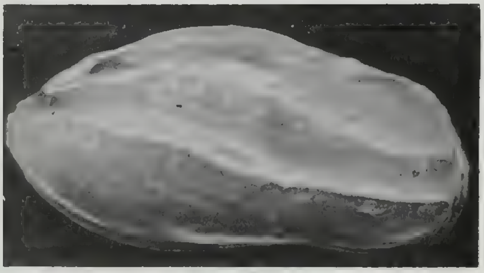
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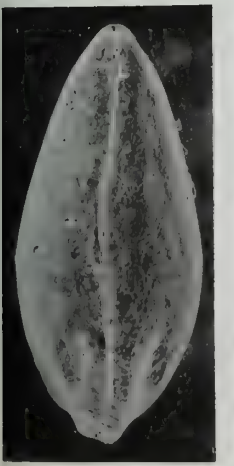

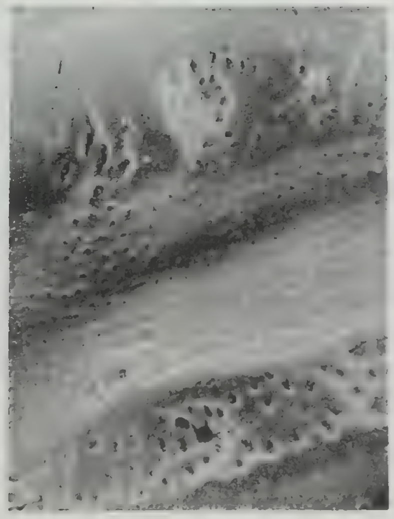
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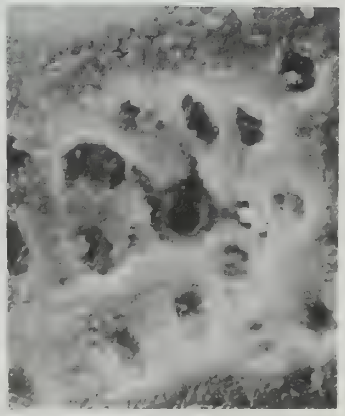


PLATE 11

× 70, except Fig. 7

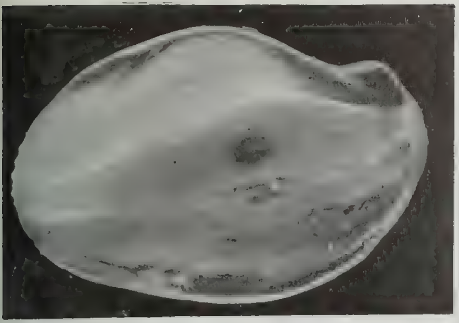
Fig. 1–4, 8, 9 ***Cytheretta forticosta*** sp. nov.

Fig. 1–4 from Upper Bracklesham Beds, Whitecliff Bay

Fig. 1 Left valve, female, Io 3871, L = 0·79; HOLOTYPE
Fig. 2 Left valve, male, Io 3872, L = 0·87
Fig. 3 Right valve, female, Io 3874, L = 0·84
Fig. 4 Right valve, male, Io 3873, L = 0·91
Fig. 8 Female carapace, ventral view, Io 3875, L = 0.80; Upper Bracklesham Beds, Selsey.
Fig. 9 Male carapace, dorsal view, Io 3876, L = 0·92; Upper Bracklesham Beds, Selsey.

Fig. 5–7 ***Cytheretta porosacosta*** sp. nov.

Fig. 5 Left valve, male, Io 3880, L = 0·79 Middle Headon Beds, Colwell Bay.
Fig. 6 Left valve, female, Io 3879, L = 0·75. HOLOTYPE; Middle Headon Beds, Colwell Bay.
Fig. 7 Enlargement of Io 3880 showing punctation × 140.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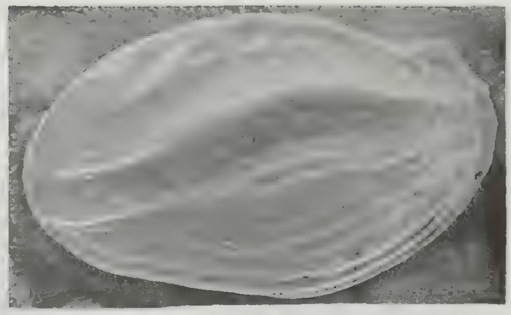
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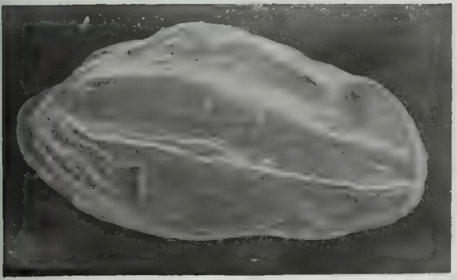
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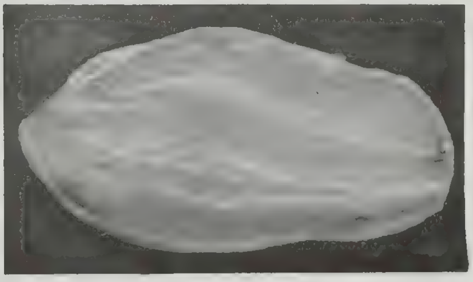
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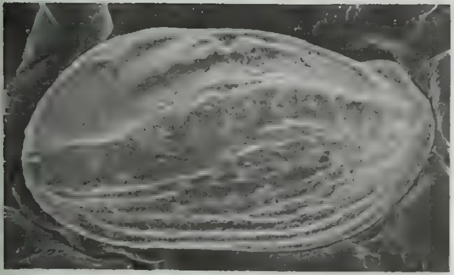
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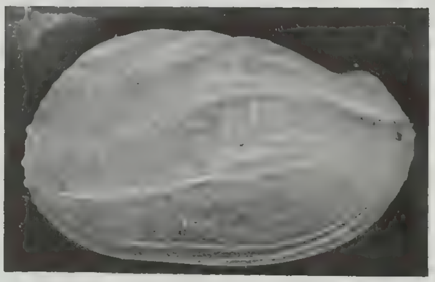
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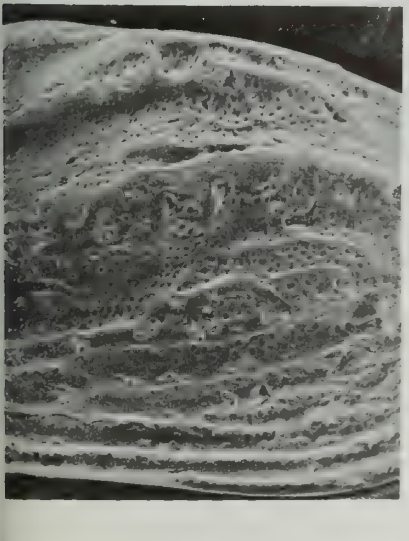

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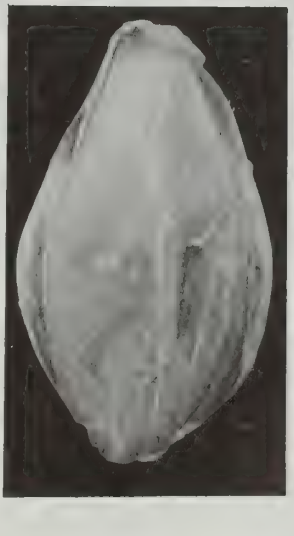

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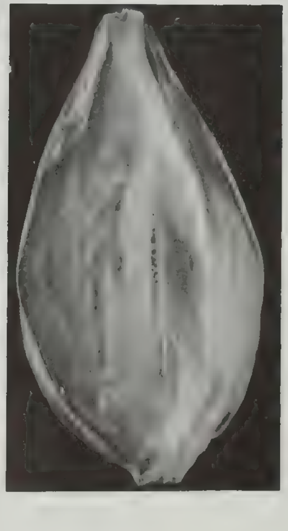


PLATE 12

FIG. 1–2, 5 ***Cytheretta laticosta*** (Reuss)

Specimens from Middle Barton Beds, Barton; × 70.

FIG. 1 Male carapace, ventral view; Io 3869, L = 0·88
FIG. 2 Female carapace, dorsal view, Io 3868, L = 0·77
FIG. 5 Left valve, female, Io 3869, L = 0·81

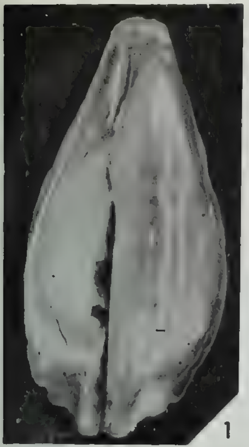
FIG. 3, 4 ***Cytheretta porosacosta*** sp. nov.

× 70

FIG. 3 Right valve, male, Io 3882, L = 0·81; Middle Headon Beds, Milford.
FIG. 4 Right valve, female, Io 3881, L = 0·76; Middle Headon Beds, Milford.

FIG. 6–12 ***Cytheretta forticosta*** sp. nov.

FIG. 6 Right valve, female, Io 3878, × 70, L = 0·86; Upper Bracklesham Beds, Selsey.
FIG. 7 Dorsal muscle scars, × 350
FIG. 8 Posterior duplicature, × 350
FIG. 9 Anterior tooth, × 350
FIG. 10 Posterior tooth, dorsal view, × 350
FIG. 11 Anterior tooth, dorsal view, × 350
FIG. 12 Central muscle scars, × 350.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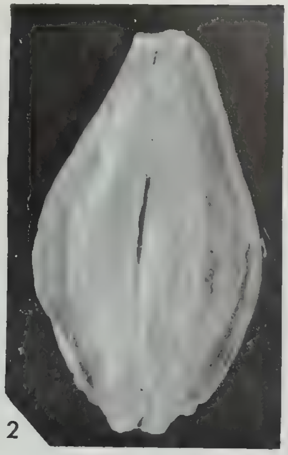
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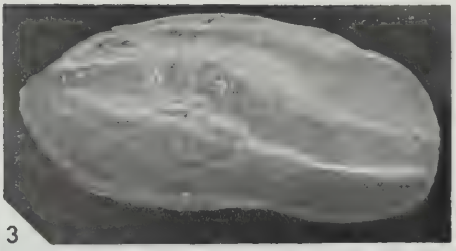
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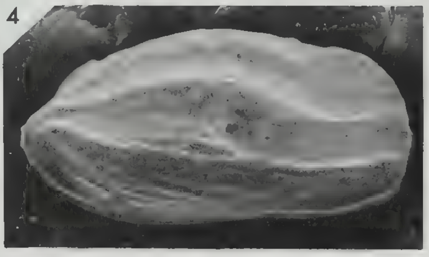
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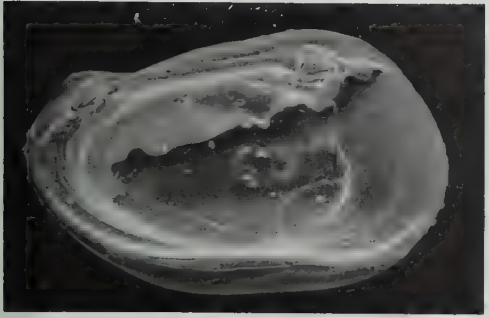
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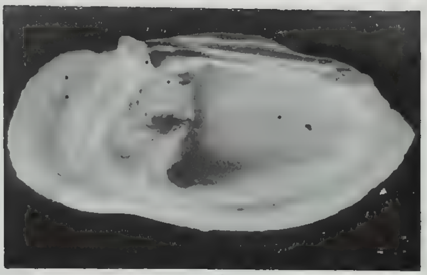
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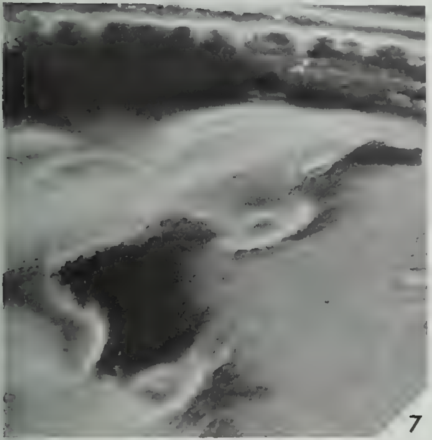
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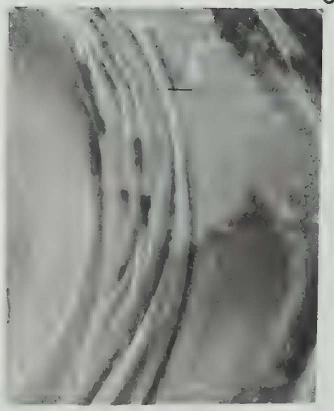
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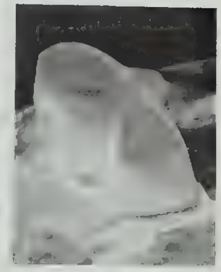
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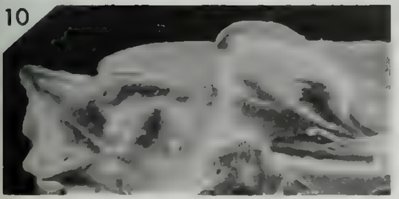
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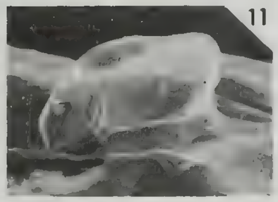
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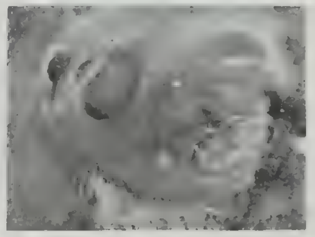
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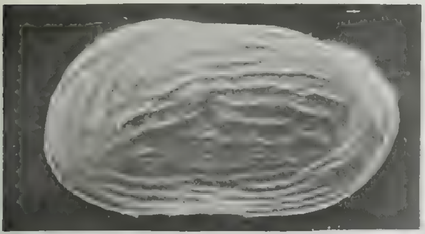
PLATE 13

Cytheretta tenuistriata ornata subsp. nov.

FIG. 1 Left valve, female, Io 3898, L = 1·03, × 50; HOLOTYPE
FIG. 2 Right valve, male, Io 4021, L = 1·14, × 50
FIG. 3 Right valve, female, Io 3899, L = 1·02
FIG. 4 Left valve, female; specimen destroyed
FIG. 5 Left valve, male, Io 4020, L = 1·15
FIG. 6 Right valve, male; specimen destroyed
FIG. 7 Left valve, 8th moult stage, L = 0·87; specimen destroyed
FIG. 8 Right valve, 8th moult stage, Io 4025, L = 0·86
FIG. 9 Left valve, 7th moult stage, L = 75·; specimen destroyed
FIG. 10 Right valve, 7th moult stage, Io 4026, L = 0·80
FIG. 11 Left valve, 6th moult stage, Io 4024, L = 0·58
FIG. 12 Right valve, 6th moult stage, Io 4027, L = 0·59

Specimens from the Falun d'Auvers-St.-Georges.



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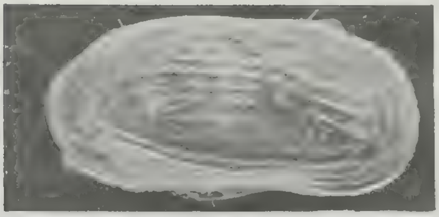

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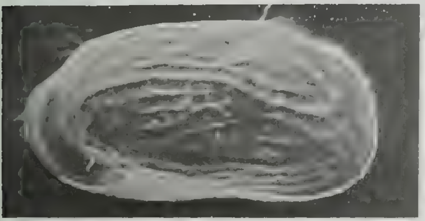

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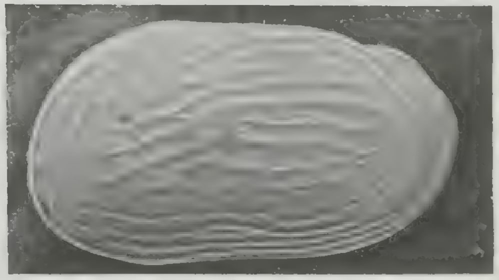

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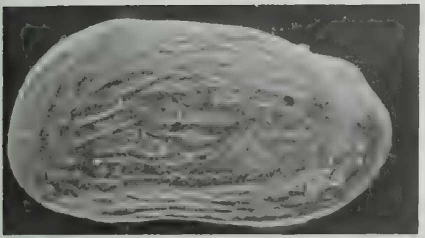

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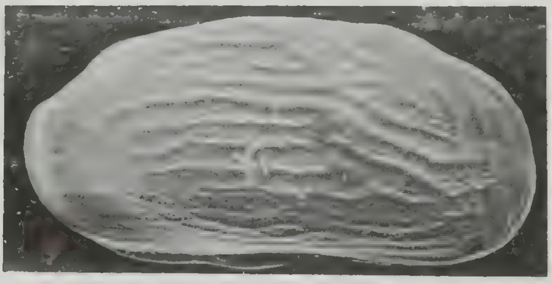

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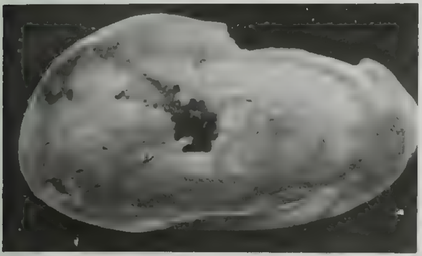

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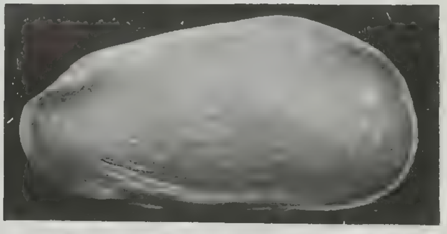

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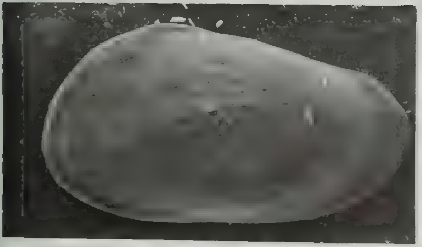

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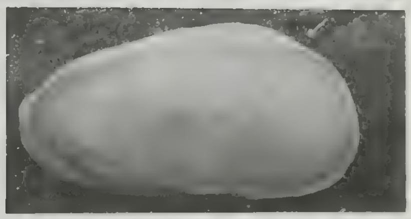

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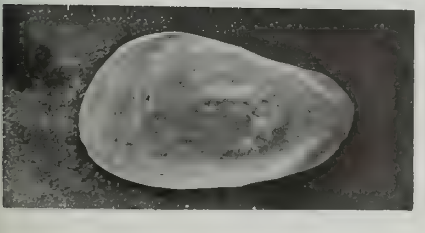

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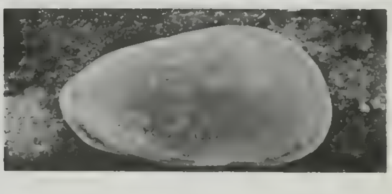

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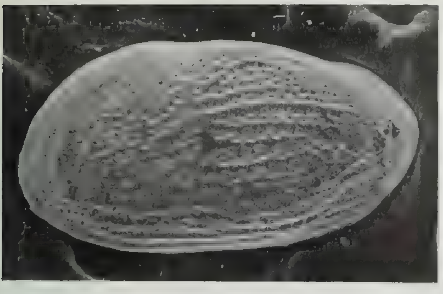
PLATE 14

Cytheretta tenuipunctata absoluta subsp. nov.

Fig. 1–4, 6, 7; × 60; specimens from the Marnes à Huitres, Cormeilles.
Fig. 1 Left valve, female, Io 3884, L = 0·84; HOLOTYPE
Fig. 2 Left valve, male, Io 3886, L = 0·98
Fig. 3 Right valve, female, Io 3885, L = 0·87
Fig. 4 Right valve, male, Io 3887, L = 0·98
Fig. 6 Female carapace, dorsal view, Io 3888, L = 0·90
Fig. 7 Male carapace, ventral view, Io 3889, L = 0·98.

Cytheretta tenuipunctata lirata subsp. nov.

Fig. 5, 8–10, × 50; specimens from the Falun d'Auvers-St.-Georges.
Fig. 5 Left valve, female, Io 3890, L = 0·90; HOLOTYPE
Fig. 8 Right valve, female, L = 0·90; specimen destroyed
Fig. 9 Right valve, male, Io 3893, L = 1·01
Fig. 10 Left valve, male, Io 3892, L = 1·04.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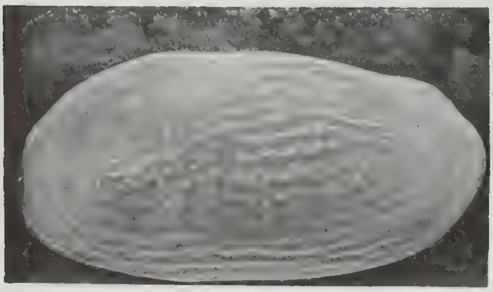
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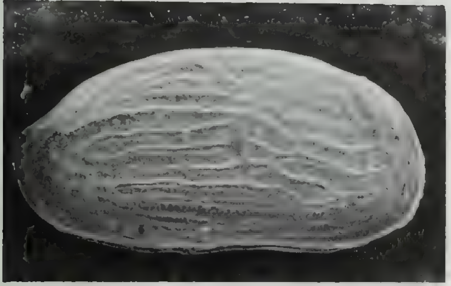
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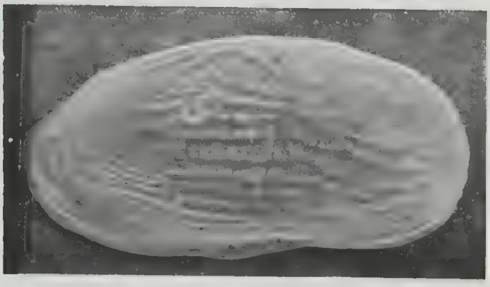
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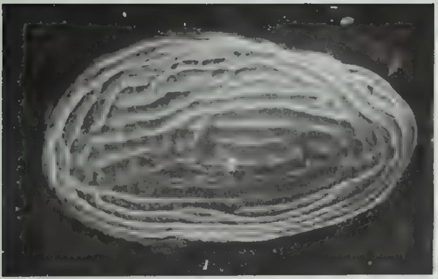
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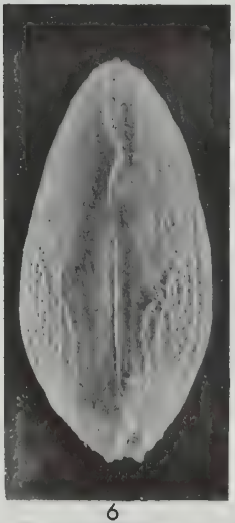
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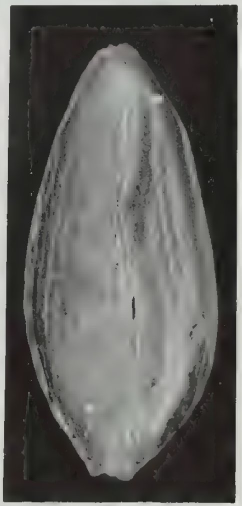
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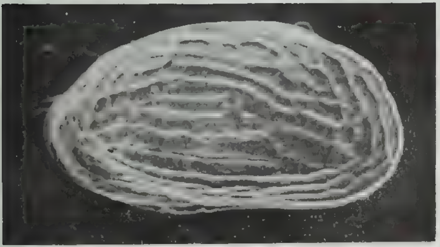
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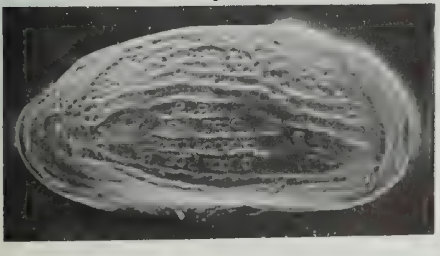
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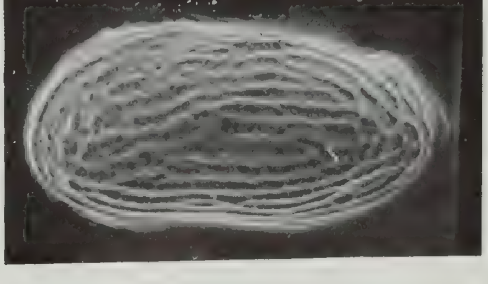
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PLATE 15

× 60, except Fig. 9, × 50

Cytheretta buttensis reticulata sp. nov., subsp. nov.

Fig. 1–8, Specimens from Cormeilles.

MORPHOTYPE A.

Fig. 1 Left valve, female, Io 4032, L = 0·85, Marnes à Huitres; HOLOTYPE

Fig. 2 Left valve, male, Io 4033, L = 0.97, Marnes à Huitres.

Fig. 3 Right valve, female, Io 4038, L = 0·82, Couches de Sannois

Fig. 4 Female carapace, dorsal view, Io 4034, L = 0·91, Marnes à Huitres

Fig. 5 Male carapace, dorsal view, L = 0·95, Marnes à Huitres. Specimen destroyed.

MORPHOTYPE B

Fig. 6 Right valve, female, L = 0·83, Couches de Sannois, Io 4036

Fig. 7 Left valve, female, Io 4037, L = 0·88, Couches de Sannois.

MORPHOTYPE C

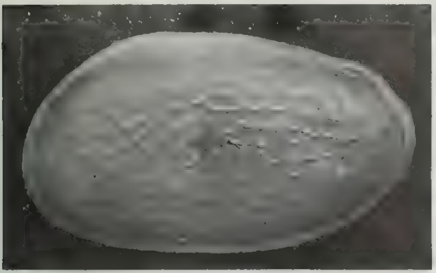
Fig. 8 Right valve, male, Io 4035, L = 0·96, Couches de Sannois

Cytheretta buttensis buttensis sp. nov.

Fig. 10 Left valve, male, Io 4031, L = 0·91, MORPHOTYPE C, Couches de Sannois; HOLOTYPE

Cytheretta tenuipunctata lirata subsp. nov.

Fig. 9 Right valve, female, L = 0·90; specimen destroyed.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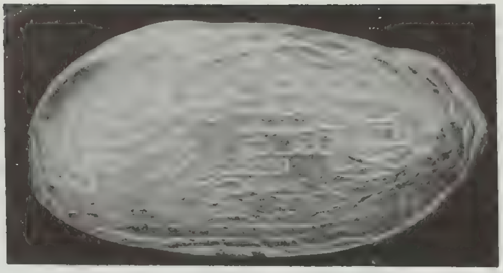
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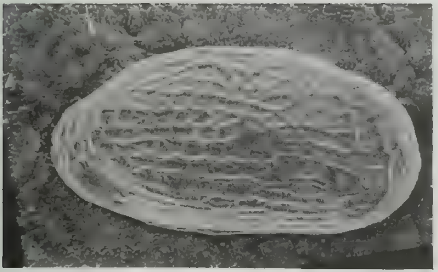
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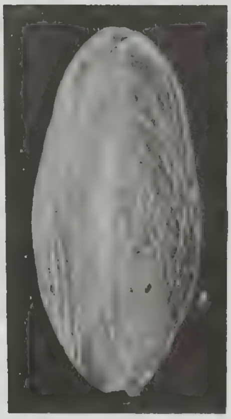
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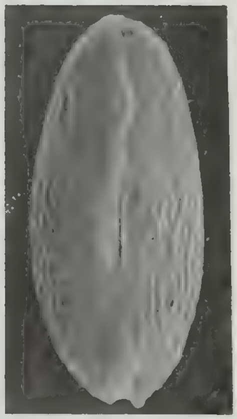
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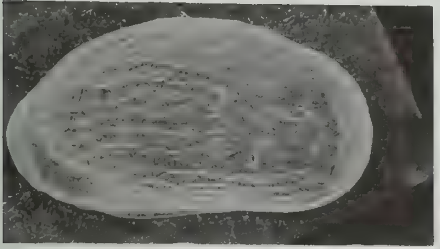
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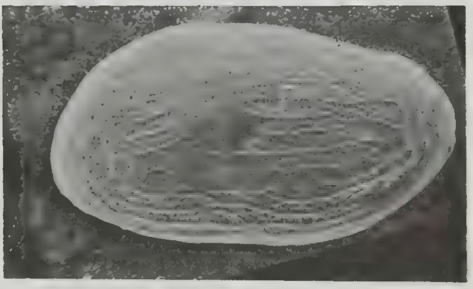
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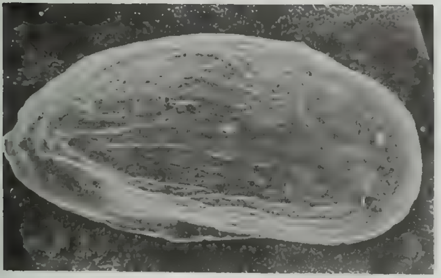
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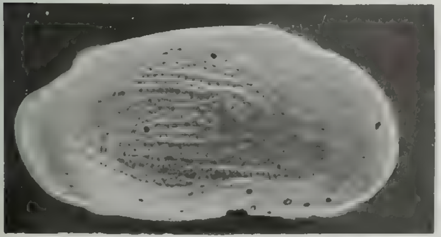
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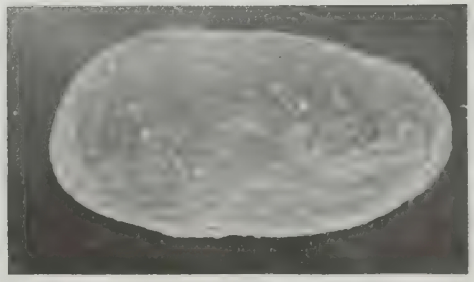
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PLATE 16

Cytheretta minipunctata sp. nov.
Fig. 1–3, × 50. Specimens from the Couches de Sannois, Cormeilles
Fig. 1 Left valve, male, Io 4028, L = 1·10. HOLOTYPE
Fig. 2 Male carapace, ventral view, Io 4028
Fig. 3 Female carapace, ventral view, Io 4029, L = 0·98.

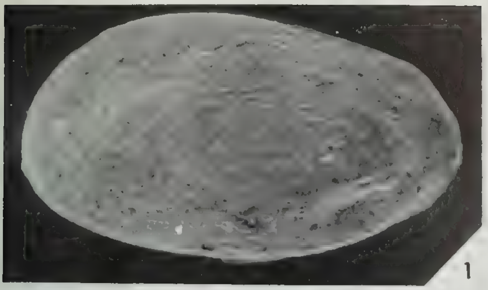
Cytheretta tenuipunctata lirata subsp. nov.
Fig. 4 Left valve, male, Io 3894, L = 1·04, × 55; Falun d'Auvers-St.-Georges.

Cytheretta tenuistriata tenuistriata (Reuss).
Fig. 5, 7 Specimens from the Unterer Meeresand, Alzey Trift
Fig. 5 Left valve, male, Io 3896, L = 1·25, × 40
Fig. 7 Right valve, female, Io 3897, L = 1·10, × 50.

Cytheretta minor (Lienenklaus).
Fig. 6 Left valve, female, Io 3704, L = 0·88; Unt. Meeresand, Alzey Trift, × 60.

Cytheretta aff. ***stigmosa Triebel.***
Fig. 8 Left valve, female, Io 4052, L = 0·76, × 65; Mid. Headon Beds, Whitecliff Bay.

Cytheretta gibberis sp. nov.
Fig. 9, 10, × 70 Specimens from the Couches du Phare, Biarritz
Fig. 9 Right valve, male, Io 4086, L = 0·92
Fig. 10 Right valve, female, Io 4084, L = 0·88; HOLOTYPE.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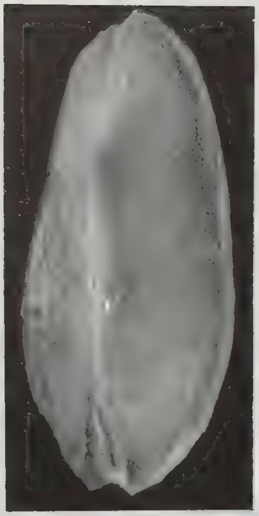
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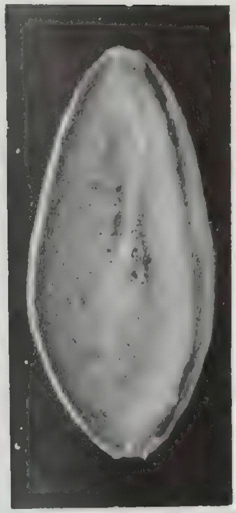
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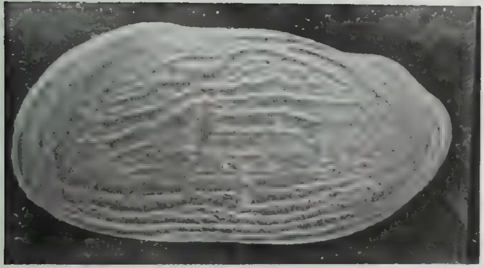
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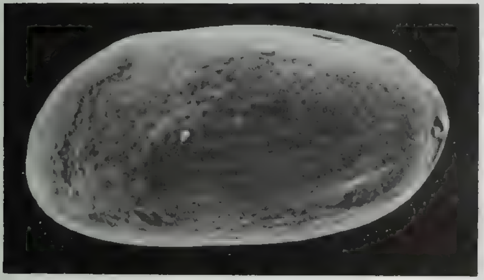
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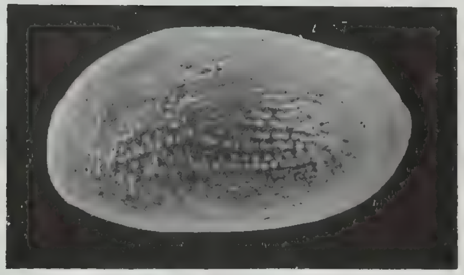
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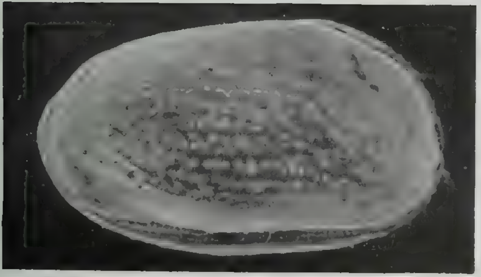
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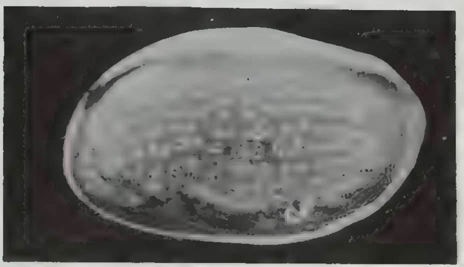
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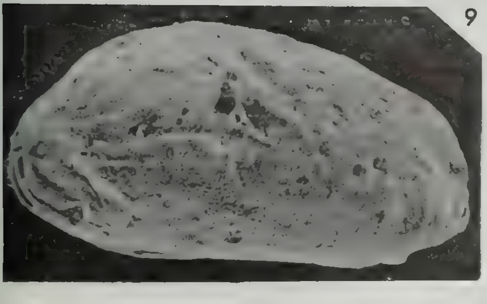
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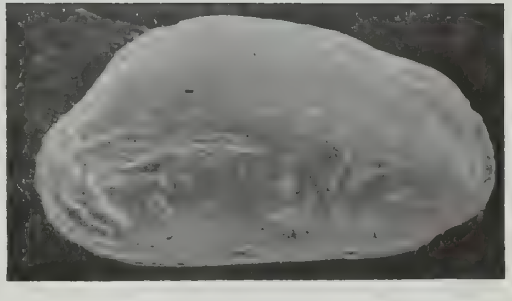
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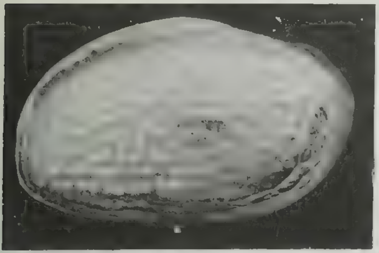
PLATE 17

Cytheretta stigmosa gallica subsp. nov.
Fig. 1, 2, 10 Specimens from the Falun d'Auvers-St.-Georges, × 60
Fig. 1 Left valve, female, Io 4053, L = 0·75; HOLOTYPE
Fig. 2 Left valve, male, Io 4055, L = 0·73
Fig. 5 Female carapace, dorsal view, L = 0·73; specimen destroyed
Fig. 10 Male carapace, dorsal view, Io 4056, L = 0·74.

Cytheretta regularis sp. nov.
Fig. 3, 4, 5, 6, 7 Specimens from the Stampian of Gaas (Lesbarritz), × 60
Fig. 3 Left valve, female, Io 4057, L = 0·70; HOLOTYPE
Fig. 4 Right valve, female, Io 4058, L = 0·68
Fig. 6 Left valve, male, Io 4059, L = 0·70
Fig. 7 Right valve, male, Io 4060, L = 0·68.

Cytheretta vesca sp. nov.
Fig. 8, 9, 12 Specimens from the Falun d'Auvers-St.-Georges, × 60
Fig. 8 Left valve, female, Io 4048, L = 0·73; HOLOTYPE
Fig. 9 Right valve, male, Io 4051, L = 0·71
Fig. 12 Right valve, female, Io 4049, L = 0·72.

Cytheretta headonensis Haskins.
Fig. 11, 13, 14 Specimens from the Middle Headon Beds, × 50
Fig. 11 Right valve, male, Io 4044, L = 0·80; Milford
Fig. 13 Left valve, male, Io 4043, L = 0·78; Headon Hill
Fig. 14 Right valve, female, Io 4046, L = 0·80; Headon Hill.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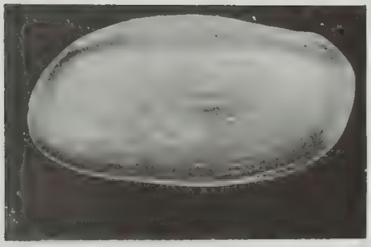
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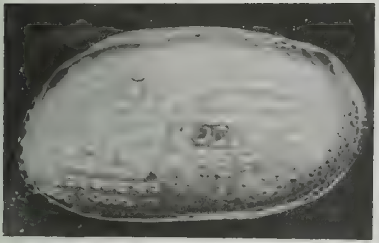
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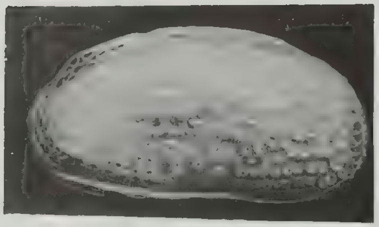
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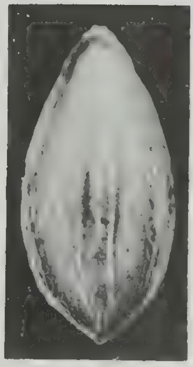
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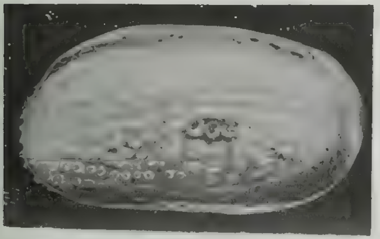
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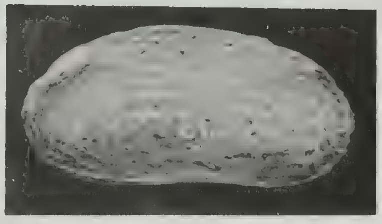
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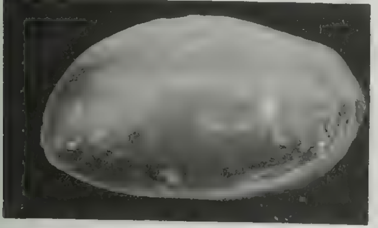
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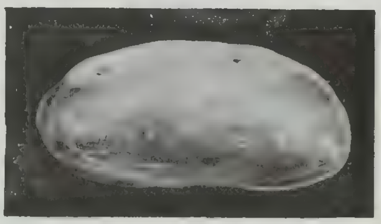
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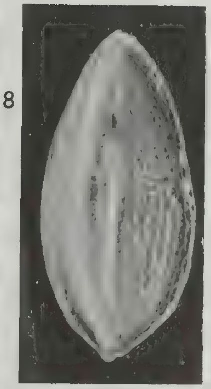
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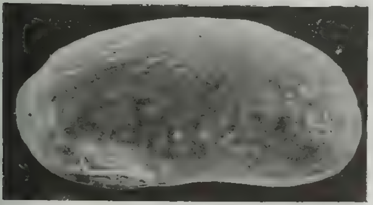
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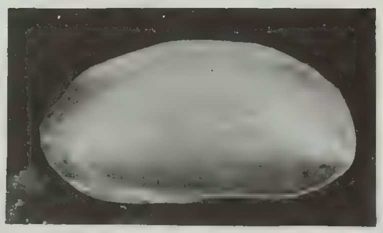
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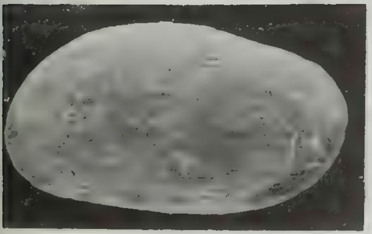
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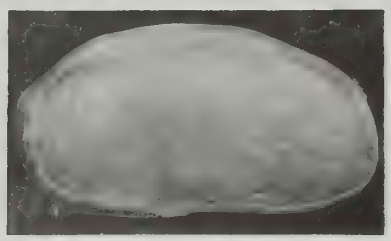
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PLATE 18

Cytheretta posticalis parisiensis subsp. nov.

Fig. 1–4, 6 Specimens from the Falun d'Auvers-St.-Georges
Fig. 1 Left valve, female, Io 4039, L = 0·95, × 50; HOLOTYPE
Fig. 2 Left valve, male, Io 4041, L = 1·05, × 50
Fig. 3 Right valve, female, Io 4040, L = 0·91, × 50
Fig. 4 Right valve, male, Io 4042, L = 1·03, × 50
Fig. 6 Anterior radial pore canals of left valve, Io 3702, × 110.

Cytheretta bullans sp. nov.

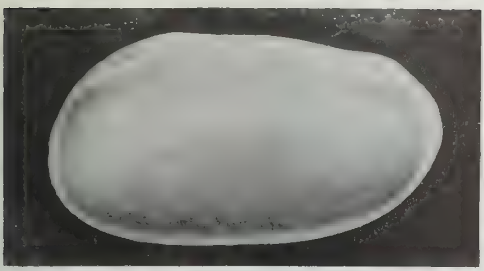
Fig. 5, 7, × 70 Specimens from the Calcaire à Algues, Blaignan
Fig. 5 Left valve, female, Io 4061, L = 0·85; HOLOTYPE
Fig. 7 Right valve, male, Io 4062, L = 0·90.

Cytheretta rhenana Triebel.

Fig. 8 Left valve, female, Io 4047, L = 0·87, × 60; Unt. Meeresand, Alzey Trift.

Cytheretta headonensis Haskins.

Fig. 9 Left valve, female, Io 4045, L = 0·83, × 70; Mid. Headon Beds, Headon Hill.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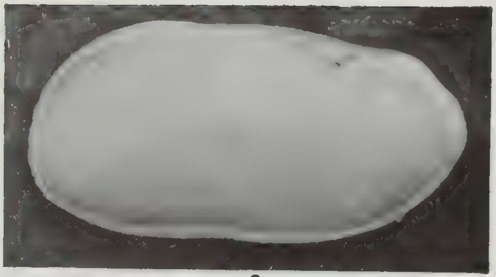
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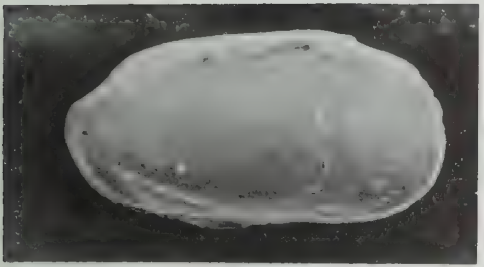
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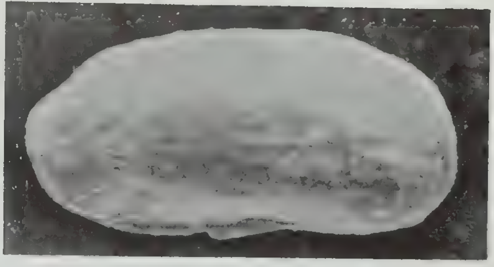
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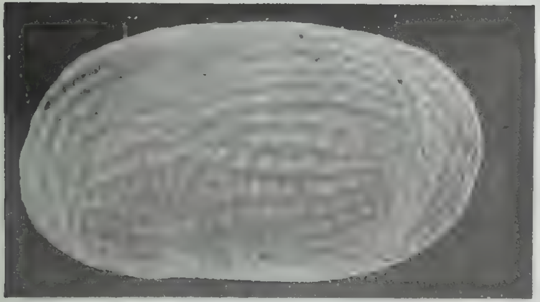
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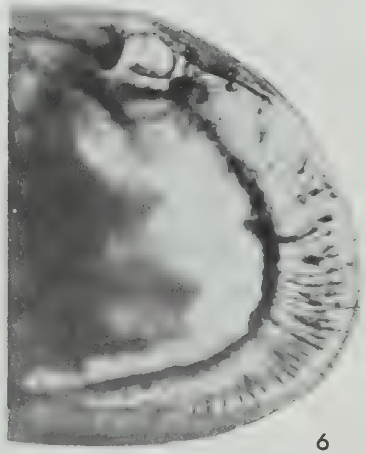
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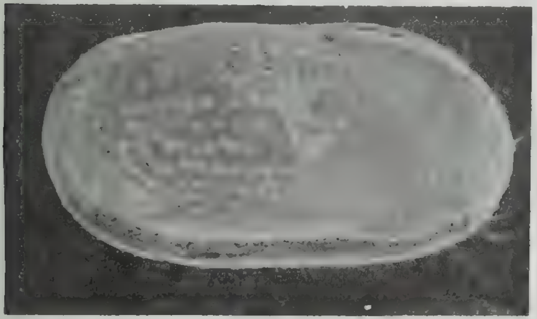
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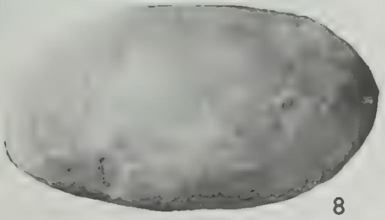
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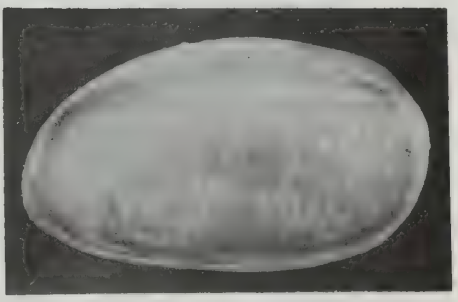
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PLATE 19

× 75

Cytheretta sagri sagri Deltel.
FIG. 1–4 Specimens from the Stampian of Gaas

MORPHOTYPE A, Gaas (Espibos)
FIG. 1 Left valve, female, Io 4063, L = 0·84
FIG. 2 Right valve, male, Io 4066, L = 0·90
FIG. 3 Right valve, female, Io 4064, L = 0·84.

MORPHOTYPE D, Gaas (Lesbarritz)
FIG. 4 Left valve, female, Io 4076, L = 0·92.

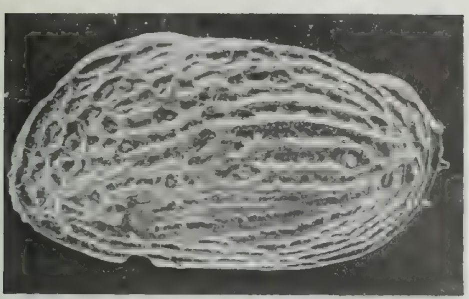
Cytheretta sagri inconstans subsp. nov.
FIG. 5–7, 9 Specimens from the Calcaire a Algues, Blaignan.

MORPHOTYPE C
FIG. 5 Left valve, male, Io 4069, L = 0·95
FIG. 6 Left valve, female, Io 4070, L = 0·95.

MORPHOTYPE B
FIG. 7 Left valve, female, Io 4067, L = 0·78; HOLOTYPE
FIG. 9 Female carapace, dorsal view, Io 4067.

Cytheretta perita Deltel.
FIG. 8 Left valve, female, Io 4089, L = 0·81; Bartonian of Le Vigneau.

Cytheretta gibberis sp. nov.
FIG. 10 Female carapace, dorsal view, Io 4085, L = 0·86; Couches du Phare, Biarritz.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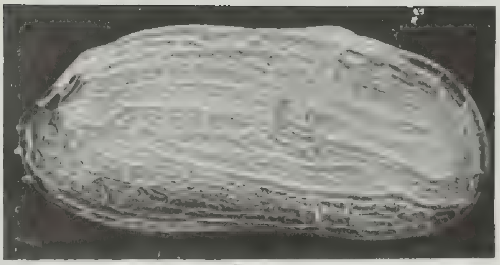
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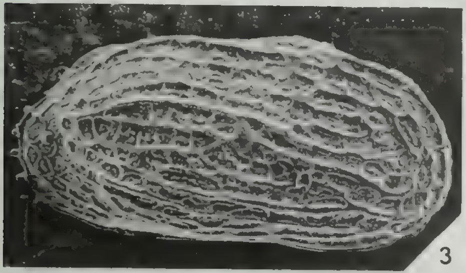
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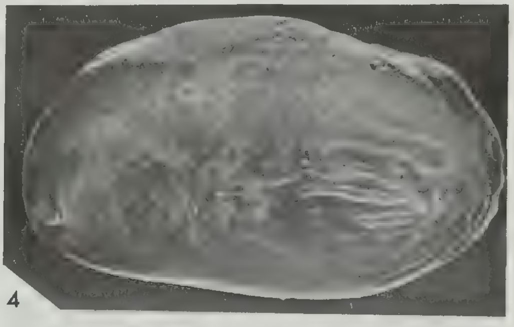
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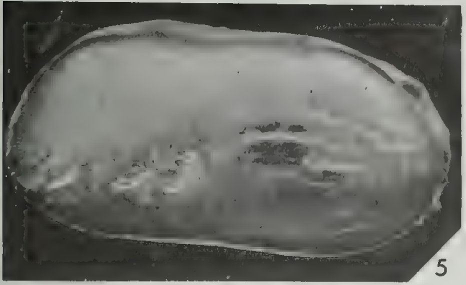
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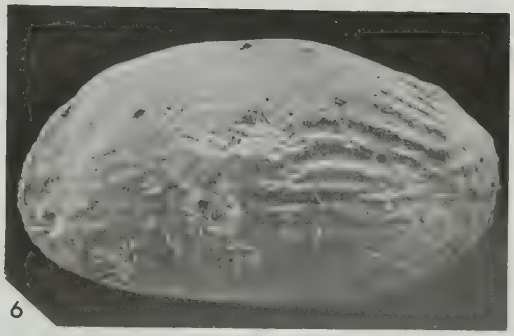
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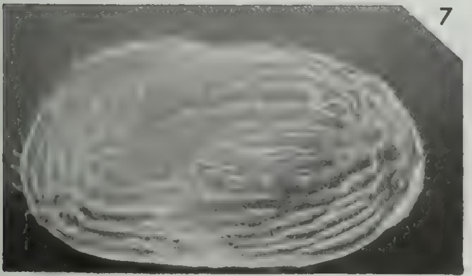
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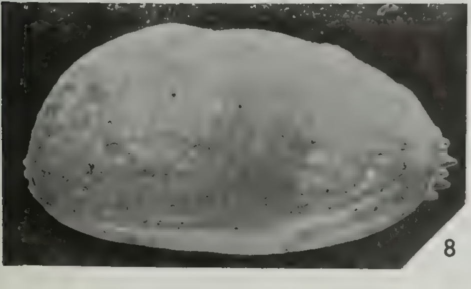
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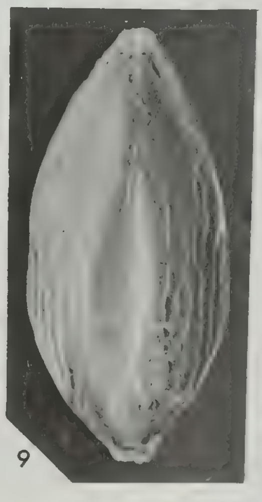
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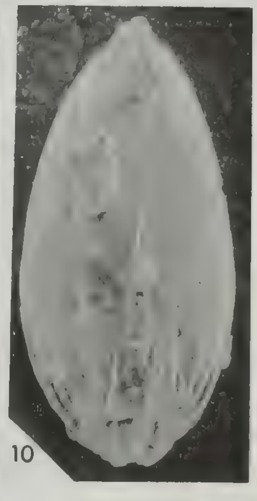
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PLATE 20

× 75

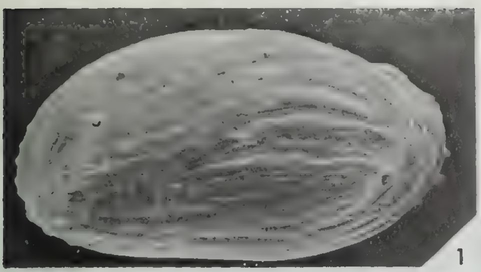
Cytheretta sagri martini subsp. nov.
FIG. 1–4 Specimens from the Couches du Phare, Biarritz

MORPHOTYPE E
FIG. 1 Left valve, female, Io 4071, L = 0·83; HOLOTYPE
FIG. 2 Right valve, female, Io 4072, L = 0·81
FIG. 3 Left valve, male, Io 4073, L = 0·86.

MORPHOTYPE F
FIG. 4 Left valve, male, Io 4074, L = 0·87.

Cytheretta postornata sp. nov.
FIG. 5–8 Specimens from the Couches de l'Atalaye, Biarritz
FIG. 5 Left valve, male, Io 4088, L = 0·84
FIG. 6 Right valve, female, Io 4087, L = 0·83; HOLOTYPE
FIG. 7 Right valve, male, Io 4088
FIG. 8 Left valve, female, Io 4087.

Cytheretta sculpta Ducasse.
FIG. 9, 10 Specimens from the Argiles à Algues, Blaignan
FIG. 9 Right valve, male, Io 4091, L = 0·73.
FIG. 10 Left valve, female, Io 4090, L = 0·70.



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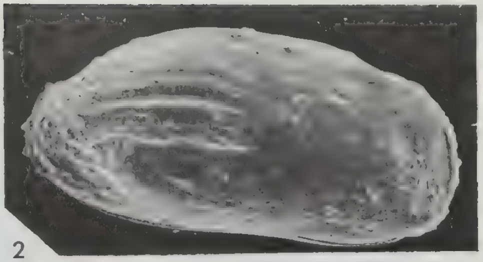

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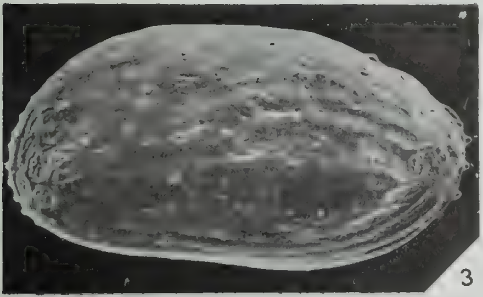

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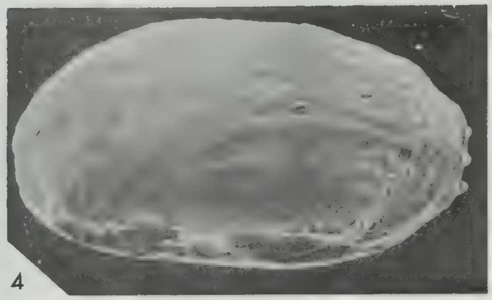

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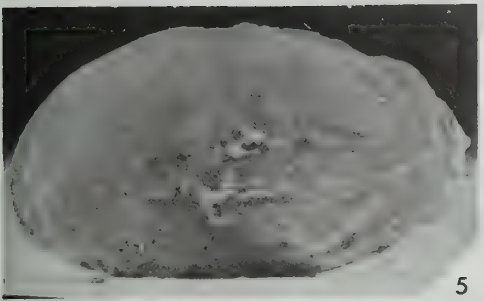

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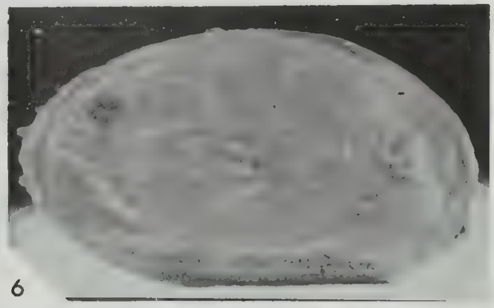

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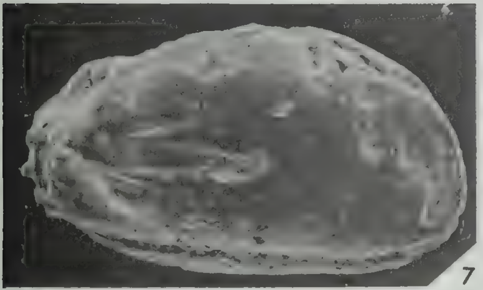

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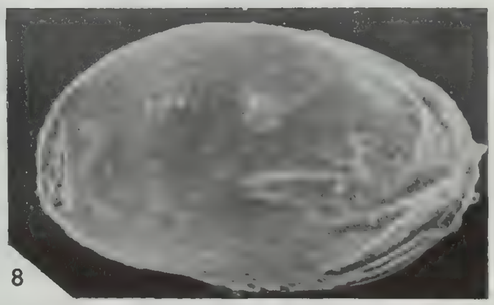

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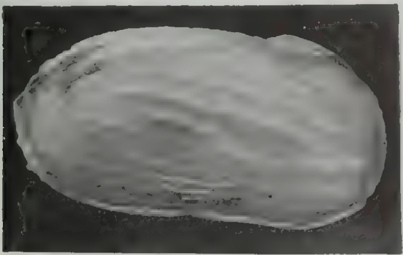

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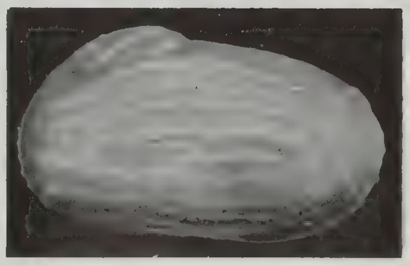

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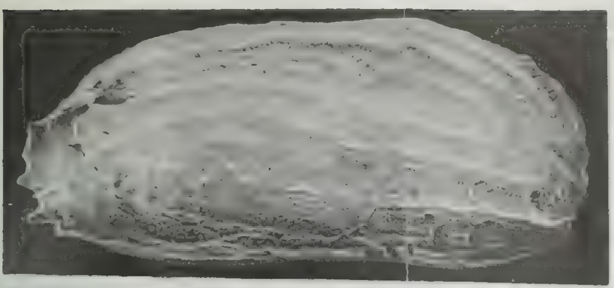
PLATE 21

× 70, except Fig. 5 which is × 160

Cytheretta minipustulosa sp. nov.
FIG. 1–4 Specimens from the Couches du Phare, Biarritz
FIG. 1 Right valve, male, Io 4080, L = 1·09; HOLOTYPE
FIG. 2 Right valve, female, Io 4082, L = 0·98
FIG. 3 Male carapace, dorsal view, Io 4081, L = 1·00
FIG. 4 Left valve, female, Io 4083, L = 0·88.

Cytheretta samothracia Deltel.
FIG. 5, 6, 8 Specimens from the Couches du Phare, Biarritz
FIG. 5 Enlargement of the antero-dorsal area of Io 4077
FIG. 6 Left valve, female, Io 4077, L = 0·95
FIG. 8 Left valve, male, Io 4078, L = 1·04.

Flexus lenijugum sp. nov.
FIG. 7, 9 Specimens from the Argiles à Algues, Blaignan
FIG. 7 Left valve, male, Io 4114, L = 0·80
FIG. 8 Right valve, female, Io 4113, L = 0·80; HOLOTYPE.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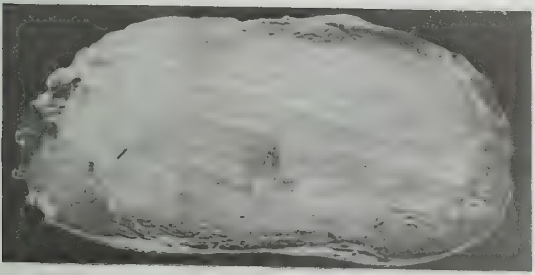
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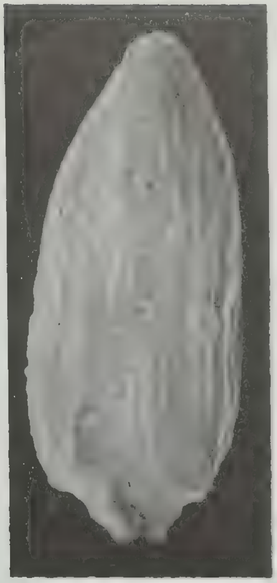
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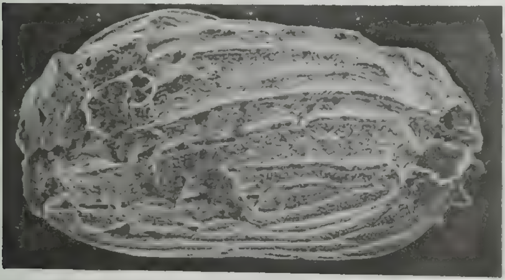
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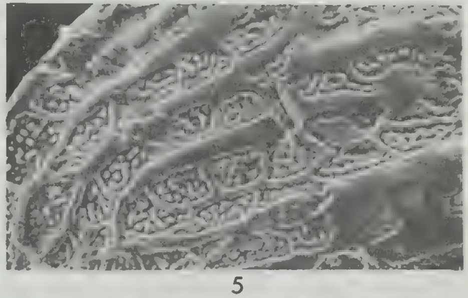
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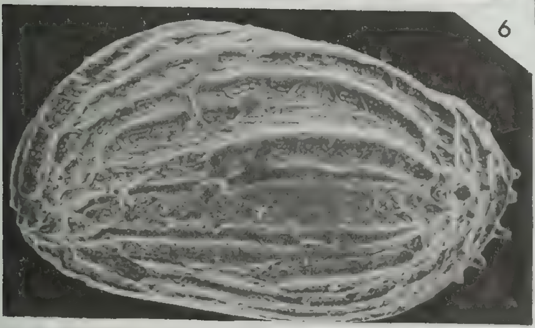
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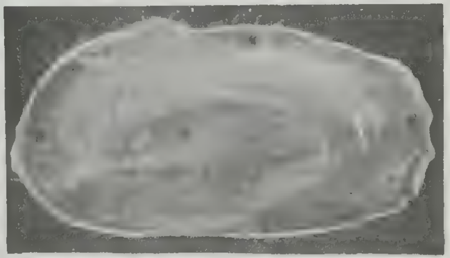
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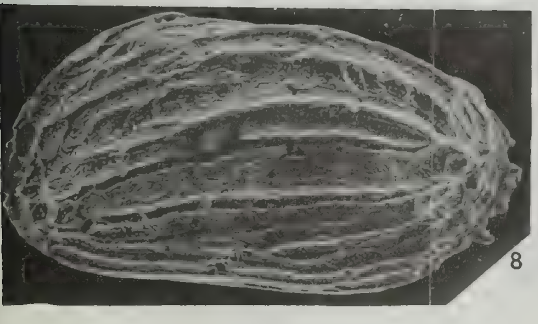
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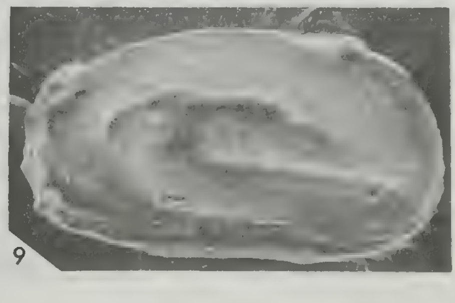

9

PLATE 22

× 60

Flexus plicatus (von Munster).
FIG. 1 Left valve, Io 4094, L = 0·80; Chattian, Astrup.

Flexus concinnus (Triebel).
FIG. 2, 3
FIG. 2 Left valve, male, Io 4095, L = 0·94; Unt. Meeresand, Alzey Trift
FIG. 3 Left valve, male, Io 4096, L = 0·81; Falun d'Auvers-St.-Georges

Flexus sp. A
FIG. 5 Left valve, female, Io 4118, L = 0·71; Sables de Lede, Bambrugge.

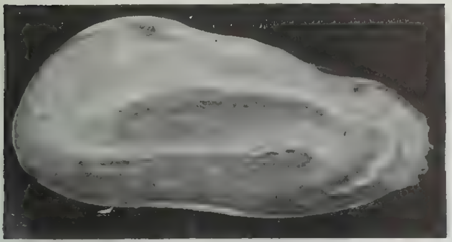
Flexus gutzwilleri (Oertli).
FIG. 4 Left valve, female, Io 4098, L = 0·79; Couches du Phare, Biarritz.

Flexus schoelleri (Keij).
FIG. 6–8 Specimens from the Faluns bleues, St. Geours-de-Maremne
FIG. 6 Left valve, female, Io 4115, L = 0·71
FIG. 7 Left valve, male, Io 4117, L = 0·74
FIG. 8 Right valve, female, Io 4116, L = 0·71.

Flexus lenijugum sp. nov.
FIG. 9, 10 Specimens from the Argiles à Algues, Blaignan
FIG. 9 Male carapace, dorsal view, Io 4114, L = 0·80
FIG. 10 Female carapace, dorsal view, Io 4113, L = 0·80; HOLOTYPE

Cytheretta bullans sp. nov.
FIG. 11 Female carapace, dorsal view, Io 4061, L = 0·85; HOLOTYPE. Calcaire à Algues, Blaignan.

Cytheretta postornata sp. nov.
FIG. 12 Female carapace, dorsal view, Io 4087, L = 0·83; HOLOTYPE. Couches de l'Atalaye, Biarritz.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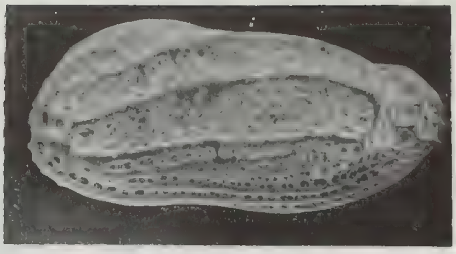
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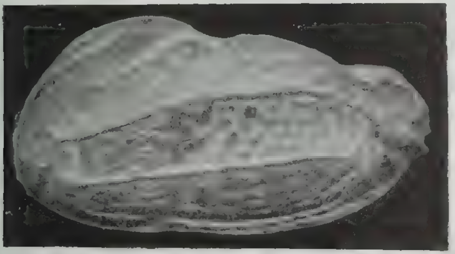
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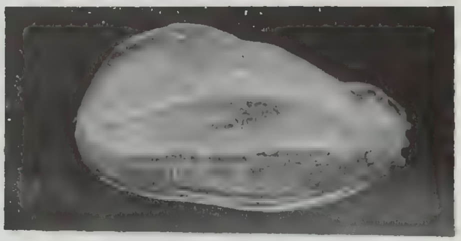
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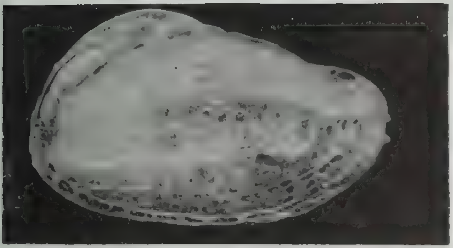
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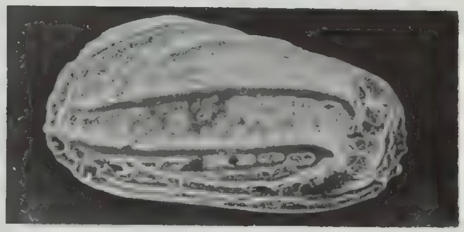
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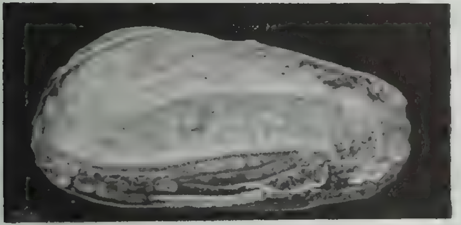
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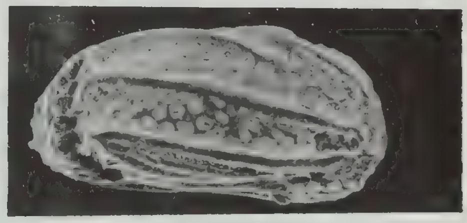
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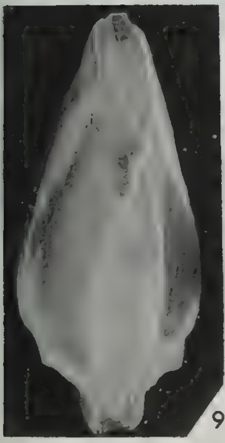
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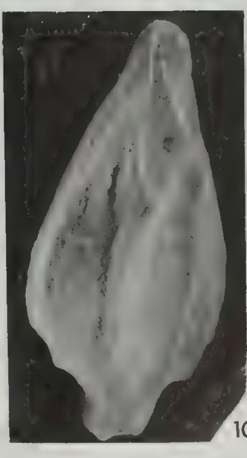
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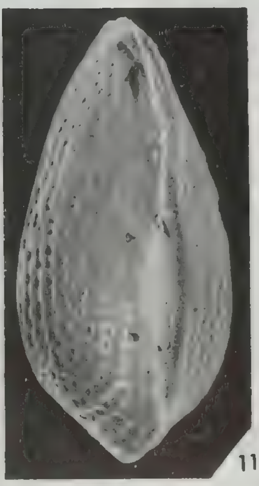
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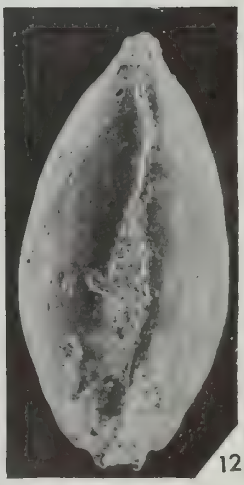
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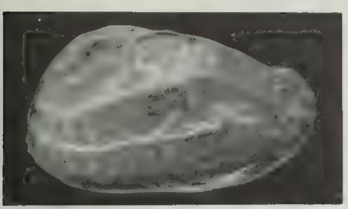
PLATE 23

× 70

Flexus ludensis sp. nov.
Fig. 1–6, 16 Specimens from the Marnes à *P. ludensis*, Verzy, except Fig. 6
Fig. 1 Left valve, female, Io 4106, L = 0·50; HOLOTYPE
Fig. 2 Left valve, male, Io 4107, L = 0·52
Fig. 3 Right valve, male, Io 4111, L = 0·51
Fig. 4 Male carapace, ventral view, Io 4109, L = 0·52
Fig. 5 Right valve, female, Io 4110, L = 0·51
Fig. 6 Left valve, male, Io 4112, L = 0·55; Mid. Headon Beds, Whitecliff Bay
Fig. 16 Female carapace, dorsal view, Io 4108, L = 0·50.

Flexus solentensis solentensis sp. nov.
Fig. 7–10 Specimens from the Middle Barton Beds
Fig. 7 Female carapace, dorsal view, Io 4101, L = 0·54; Alum Bay
Fig. 8 Left valve, Io 4101
Fig. 9 Right valve, female, L = 0·51; Barton; specimen destroyed
Fig. 10 Left valve, male, Io 4100, L = 0·54; Barton; HOLOTYPE.

Flexus solentensis congestus subsp. nov.
Fig. 11–15 Specimens from the Upper Barton Beds, Barton
Fig. 11 Left valve, female, Io 4103, L = 0·51; HOLOTYPE
Fig. 12 Male carapace, ventral view, Io 4104, L = 0·54
Fig. 13 Left value, Io 4104
Fig. 14 Right valve, female, Io 4105, L = 0·51
Fig. 15 Male carapace, anterior view, Io 4104.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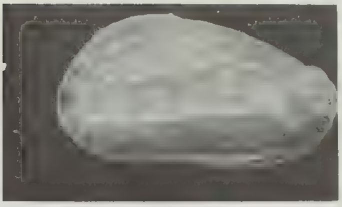
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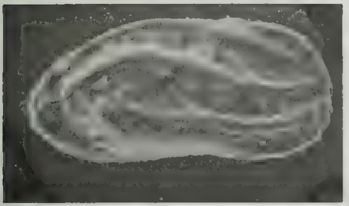
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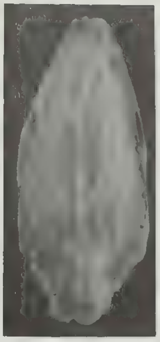
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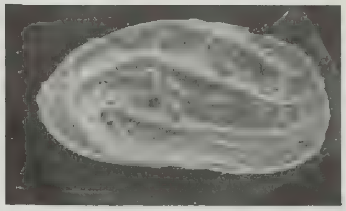
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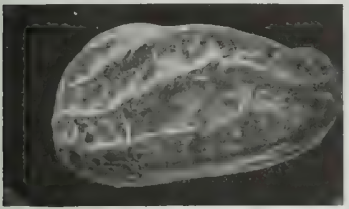
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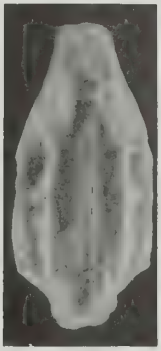
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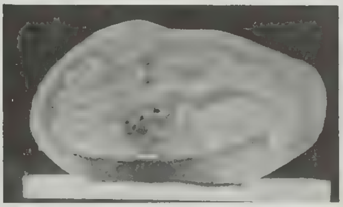
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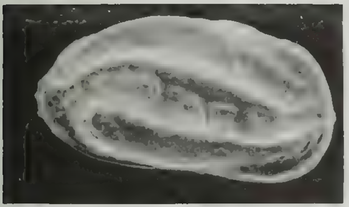
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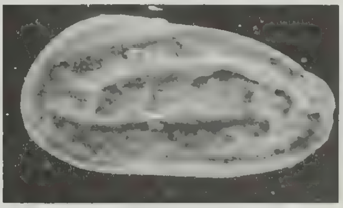
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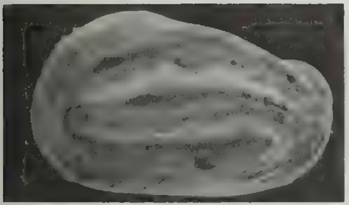
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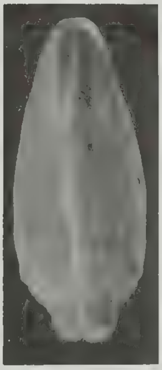
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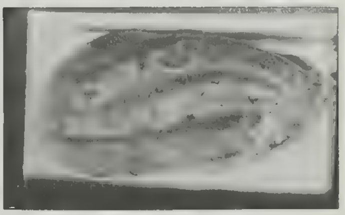
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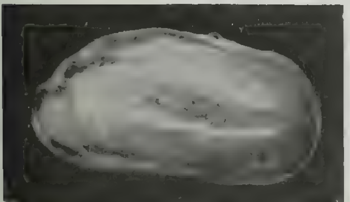
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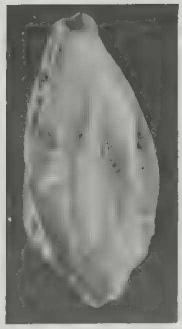
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